

Geographical variation in morphology and voice of Three-striped Warbler *Basileuterus tristriatus*

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SUMMARY.—Plumage and vocal variation were studied in a widespread New World passerine, Three-striped Warbler *Basileuterus tristriatus*. Two parallel north–south clines or step-clines in underparts coloration occur in the Central and East Andes of Colombia, with yellower specimens at northern latitudes in both ranges. In the East Andes, the cline is reversed further north, where paler-bellied birds occur. Most West Andes and west-slope specimens differ from those in the Central and East Andes in their more olivaceous flanks (although some show underparts similar to Central Andes specimens). *B. t. daedalus* can be restricted to the West Andes based on ‘75%’ subspecies concepts but not those requiring diagnosability. Andean *B. tristriatus* possess at least three vocalisation types: (i) a rising song starting with a trill and ending in scratchy notes; (ii) a slow song comprising jumbled notes; and (iii) calls of repeated, simple, single notes. West and Central Andes populations are vocally similar and differ non-diagnosably from East Andes populations in the speed of the trill in rising songs. Specimens from Serranía de San Lucas, Colombia, are morphologically similar to northern Central Andes birds, but the rising song has a shorter introductory trill and neither song attains such low minimum acoustic frequencies. Santa Marta Warbler *B. basilicus* has very different songs comprising low-pitched, slow, incessant, complex notes, is mildly differentiated in biometrics and strongly differentiated in plumage from *B. tristriatus*, supporting its current specific treatment. The rising song of Three-banded Warbler *B. trifasciatus* lacks an initial trill and its slow song has a different note shape to *B. tristriatus* but further research in a potential contact zone in southern Ecuador is required. Within *B. tristriatus*, northernmost populations assigned to *melanotis* and *chitreusis* in Costa Rica and western Panama give only the ‘slow song’ type, but these are delivered diagnosably faster than in any other population. *B. t. tacarcunae* from eastern Panama and north-western Colombia has a different song, comprising an incessant, long jumble of notes interspersed with short churrs. Populations either side of the Huancabamba depression in Peru show only minor differences in voice, but those either side of the Apurímac show significant but non-diagnosable differences in song speed. Bolivian populations have strikingly different rising songs that are quantitatively diagnosable. The rising song of Venezuelan Three-striped Warblers recalls that of *B. trifasciatus* in its slow delivery. Differences in vocal repertoire and quantitative measures support species rank for Costa Rican Warbler *B. melanotis* and Tacarcuna Warbler *B. tacarcunae*. Bolivian Warbler *B. punctipectus* is also a candidate for species rank.

Three-striped Warbler is widespread and locally common in premontane to montane forests of the Andes and elsewhere, from Costa Rica and northern Venezuela south to Bolivia. Many subspecies are currently recognised, all of them described >60 years ago. These are, from north to south: *melanotis* Lawrence, 1868 (type locality: Cervantes / Birris, Costa Rica), *chitreusis* Griscom, 1927 (Veraguas, western Panama), *tacarcunae* Chapman, 1924 (Tacarcuna





Legend to plates on facing page and above

Figure 1. Variation in Three-striped Warbler *Basileuterus tristriatus* in the Colombian Andes. Tacarcuna (*tacarcunae*): A. Cerro Tacarcuna, Chocó (© J. M. Ruíz-Ovalle / Fundación Ecotrópico, Colombia). West Andes (*daedalus*): B. RNA Loro Orejiamarillo, Jardín, Antioquia (© G. Suárez / ProAves). C. RNA Eriocnemis, Munchique, Cauca (© ProAves). D. RNA Pangan, Nariño (© J. C. Luna / ProAves). San Lucas (subsp.): E–F. Santa Cecilia, Bolívar (© B. Huertas / Colombian EBA Project) (different individuals). Central Andes (*daedalus*): G. Cay, Ibagué, Tolima (© A. Quevedo / ProAves). H. Cascada, Tolima (© Photographer unknown / ProAves). East Andes (*auricularis*): I. El Talismán, Serranía de los Yariquíes, Santander (© B. Huertas / Colombian EBA Project). J. Virolín, Santander (© N. Silva / ProAves). K. Serranía de los Churumbelos, Cauca (© P. Salaman / Colombian EBA Project). Head of Magdalena Valley (*auricularis*): L. Finca Merenberg, Huila (© P. Salaman / Colombian EBA Project).

Mountains, southernmost Panama), *pariae* Phelps & Phelps Jr., 1949 (Paria Peninsula, Sucre, Venezuela), *bessereri* Hellmayr, 1922 (Caracas, Venezuela), *meridanus* Sharpe, 1885 (Mérida, Venezuela), *auricularis* Sharpe, 1885 ('Bogotá'), *daedalus* Bangs, 1908 (San Antonio, río Cali, Colombia), *baezae* Chapman, 1924 (Baeza, east Ecuador), *tristriatus* (Tschudi, 1844) (Junín, Peru), *inconspicuus* J. T. Zimmer 1949 (Inca Mine, Inambarí Valley, [presumably = Cerro Inca Mina, Puno], southern Peru), *punctipectus* Chapman, 1924 (Cochabamba, Bolivia) and *canens* J. T. Zimmer 1949 (Samaipata, Santa Cruz, Bolivia) (Hellmayr 1935, Dickinson 2003, Curson

et al. 1994, Restall *et al.* 2006, Curson 2010). Because a useful map of its distribution was published recently by Gutiérrez-Pinto *et al.* (2012), none is given here.

Currently recognised subspecies differ mainly in shade of their underparts and head-stripes, which vary between yellow, orange, buffy and grey, and base colour to the head, which is black, dusky or olivaceous. Some Central American populations also differ in their upperparts coloration, whilst those in southernmost Peru and Bolivia have speckled breasts (Curson *et al.* 1994). Two taxa treated as separate species but which have been considered related are Santa Marta Warbler *B. basilicus* (Todd, 1913) of the Santa Marta Mountains in Colombia and Three-banded Warbler *B. trifasciatus* Taczanowski, 1880, which occurs in drier habitats on the west slope of the Andes in south-west Ecuador (subspecies *nitidior* Chapman, 1924) and north-western Peru (nominate).

Ornithologists have long been puzzled by the phenotype of *B. tristriatus* populations in the northern Central Andes. Chapman (1924) noted that a specimen from La Frijolera, Antioquia, Colombia (AMNH 134101) was an 'interesting exception' due to its bright yellow underparts. He considered '...that our remaining thirty Colombian specimens agree essentially among themselves and that not one closely approaches the Ecuadorean, not to mention Peruvian, bird indicates ... that the high colors of the Antioquia specimen are only a striking example of individual variation'. Todd (1929) disagreed, considering that it would be 'odd to find an individual with the characters of another and very different form turning up within the range of an ally'. Zimmer (1949) did not assign this specimen to any subspecies, noting that: 'it may be that a series of specimens from the region of La Frijolera would show a resident population with the characters of this unique example. Such a series ... should be secured and studied before final disposition of the case is made'. Hellmayr (1935) did not comment on the Frijolera specimen, but confusingly listed it both under nominate *tristriatus* (as per Chapman's comparison) and subspecies *daedalus*.

No-one conducted any study into *B. tristriatus* of the nature proposed by Todd (1929) until Salaman *et al.* (2001a) reached the lower montane slopes of Serranía de San Lucas, an isolated mountain range north of the Central Andes. We trapped several Three-striped Warblers, preparing two specimens, which we considered 'may relate to an undescribed subspecies' with 'bright yellow underparts'. Salaman *et al.* (2002) subsequently considered that birds in San Lucas 'differ from ... subspecies of the three Colombian Cordilleras, with brighter and more extensive yellow underparts' and 'represent an undescribed subspecies', but did not provide a name. Curson (2010) also referred to this population as undescribed.

Since Salaman *et al.* (2001a, 2002) rediscovered the northern, yellow-bellied population of *B. tristriatus*, I have been collating data to assess geographical variation in voice and morphology of *B. tristriatus* in Colombia and elsewhere. In January 2010, during another expedition to the San Lucas highlands (see Donegan 2012), six individuals were mist-netted, all of which had bright yellow underparts (Fig. 1E–F). Sound-recordings of all three main vocalisation types were made (Figs. 3A, 5E–F, 7E–F). These materials, together with other recent specimen and mist-net data, facilitate a better understanding of geographical variation in voice and plumage in the group.

In a molecular phylogenetic study of *B. tristriatus*, Gutiérrez-Pinto *et al.* (2012) found that the San Lucas specimens occupy a basal position with respect to other north Andean populations. Morphologically similar birds in the northern Central Andes referred to the same population as the Frijolera specimen clustered with other Central Andean specimens. The molecular study was published after a previous iteration of this manuscript had been submitted for publication and reviewed. This paper was revised to discuss the molecular study. Because Gutiérrez-Pinto *et al.* (2012) have declared their intent to 'present a description of [the San Lucas] new taxon elsewhere', I refrain from making such a designation here.

Methods

Specimens were studied at the following institutions: American Museum of Natural History, New York (AMNH); Natural History Museum, Tring (BMNH); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá (ICN); Universidad Industrial de Santander (UIS); and Smithsonian Institution, National Museum of Natural History, Washington (USNM). Details of studied specimens appear in Appendix 3. Biometric data were taken only at BMNH, AMNH, ICN and UIS. The following measurements were taken: wing-chord and tail length (to nearest mm), tarsus length, culmen length from skull to tip (to nearest 0.5 mm) and, from specimen labels, mass (g), where available. Biometric data from my field work in all three Andean cordilleras with additional mist-net data from ProAves were also analysed.

Biometric and vocal data were subdivided according to currently recognised subspecies, well-known biogeographic divides and the phylogeny of Gutiérrez-Pinto *et al.* (2012). Various diagnosability tests were undertaken for pairs of biometric and vocal variables, following Donegan (2008). For biometrics, three separate analyses were conducted using different datasets: (i) live capture data; (ii) all specimens; and (iii) male specimens.

Sound-recordings assumed to involve *B. basilicus*, *B. trifasciatus* and all described subspecies of *B. tristriatus* except *pariae* were studied (Appendix 3). Recordings were sorted geographically and by vocal type, then compared using subjective criteria (note shape and song structure) and quantitative data using the methodology detailed in Appendix 2.

Most *B. tristriatus* populations possess three different types of vocalisations (Schulenberg *et al.* 2007). The best-known song ('rising song': Figs. 3–4) usually commences with a fast trill ('A' in Fig. 3C), comprising notes of narrow bandwidth, which becomes slower in speed, wider in bandwidth and higher pitched, then usually disintegrates into a series of more scratchy, individually audible notes ('B' in Fig. 3C). A separate vocalisation ('slow song': Fig. 5) is similar in some populations to the last part of rising song, being a series of individually audible, jumbled, scratchy notes of variable acoustic frequency and note shape. In some recordings, the slow song follows shortly after, or is delivered at the same time as a rising song in a duet. As noted by Schulenberg *et al.* (2007), the rising song appears to be given by males and slow song by females, but this is difficult to confirm due to the lack of sexual dichromatism. Finally, all populations give sharp *tsip* notes ('call': Fig. 7). These are given intermittently while foraging but are delivered in more rapid succession in alarm or flight. Other calls with notes similar to individual notes in songs are also sometimes given. Fast, short, high-pitched trills are also particularly prevalent in the East Andes, but were not measured given the small to non-existent samples for most populations. The description by Curson *et al.* (1994) of a *che-weep* call does not relate to any vocalisation in my sample.

Geographical variation in plumage of *B. tristriatus*

Central America.—The northernmost population, *B. t. melanotis*, is restricted to montane Costa Rica. Ridgway (1902) treated it as a separate species. Subspecies *chitrensis* (which is junior to *melanotis*) was described from the same mountain complex but further east. It differs in having darker posterior underparts and flanks. Both subspecies have browner upperparts than other taxa, with a more buffy (almost orange) crown-stripe and supercilium (Curson *et al.* 1994).

B. t. tacarcunae is based on a type collected on the Panamanian side of Mt. Tacarcuna (Chapman 1924) and occurs at higher elevations in the Darién and San Blas region of Panama, as well as just inside Colombia. It has a buffy-yellow crown-stripe, more olivaceous head coloration and darker, greener underparts than Andean birds (Figs. 1A, 2). Compared

to *chitrensis*, it has a more olivaceous head, more orange crown-stripe and yellower throat (Curson *et al.* 1994).

Venezuela.—Populations on the Paria Peninsula, in montane Sucre, the Coastal Cordillera and Mérida Andes are mildly differentiated from one another in plumage, but have greyish face-sides, in contrast to the uniform black or dusky head elsewhere in the Andes. They also have dull greyish or cream, not yellow, underparts.

The northern Andes.—In the Colombian Andes, plumage variation in *B. tristriatus* is complex. The main differences are in coloration of the underparts and forecrown, which are concolorous in most populations. There is no consensus concerning the recognition or distribution of subspecies in the region.

The type specimen of *daedalus* was collected along the río Cali, in the West Andes (dpto. Valle del Cauca), so this name is available for westernmost populations. Chapman (1924) treated *daedalus* as a synonym of *auricularis* (a name based on a specimen from the East Andes: see below), and was followed by Meyer de Schauensee (1964) and Hilty & Brown (1986). However, Todd (1929), Hellmayr (1935, 'with considerable reluctance'), Zimmer (1949), Ridgely & Greenfield (2001), Salaman *et al.* (2001b, 2010), Krabbe & Nilsson (2003), Restall *et al.* (2006) and McMullan *et al.* (2010, 2011) all recognised *daedalus* for Colombian West Andes and west Ecuadorian populations. The largest museum collections of Colombian birds are also inconsistent in this respect: in BMNH and ICN, specimens labelled *daedalus* are restricted to the West Andes and west slope, whilst at USNM, specimens from the West and Central Andes bear this name and at AMNH all Colombian material is labelled *auricularis*.

West Andes and west Ecuadorian specimens have a darker and more extensive olivaceous wash to the flanks than those from the Central and East Andes or east slope (Fig. 8). However, a handful of West Andes specimens at ICN and AMNH are indistinguishable in underparts coloration from Central Andes birds from Quindío. Owing to a predominance of specimens with olivaceous flanks, *B. t. daedalus* can be restricted to the West Andes and western slope under 75% subspecies concepts but not under those requiring diagnosability. Fjeldså & Krabbe (1990) and Curson (2010) considered *daedalus* also to occur on the west slope of the Central Andes, with *auricularis* replacing it on the east slope of that range. This hypothesis is not supported, as discussed below. Curson *et al.* (1994) considered *daedalus* to occur broadly over the Central Andes and restricted *auricularis* to the East Andes and east slope.

Striking north / south variation in underparts coloration is evidenced by specimens from both the Central and East Andes and eastern Ecuador (Fig. 2). Various names are available for East Andes and east slope populations. The oldest, *tristriatus*, has its type locality in Junín, Peru, but is widely considered to range north to southern Ecuador (e.g. Ridgely & Greenfield 2001).

According to the original description (Sharpe 1855), *auricularis* has 'paler and duller' underparts than nominate *tristriatus*. The *auricularis* type (and other 'Bogotá' specimens at AMNH) are consistent with more recent East Andes specimens from Cundinamarca to Boyacá, so the null hypothesis of a Colombian East Andes locality for 'Bogotá' specimens is not contradicted. The most junior name for birds in this region, *baezae*, has been applied to populations with rather bright yellow underparts on the Ecuadorian east slope. Topotypical material pertaining to all these names is quite distinct in plumage. However, Ecuadorian specimens with underparts intermediate between 'Ecuadorian *tristriatus*' and '*baezae*' are present in collections and widely reported in the literature (e.g. Ridgely & Greenfield 2001).

A specimen from the southernmost East Andes (Serranía de los Churumbelos) has equally dull underparts as those from Cundinamarca and northern Ecuador (Figs. 1K, 2).

Similar specimens occur at the head of the Magdalena Valley in the southernmost Central Andes of dpto. Huila (Fig. 1L). As is the case for many species in the East Andes, there is a notable lack of specimens (and sound-recordings) from between Churumbelos (dpto. Cauca) and the Picachos depression (dpto. Meta), although little variation is evident between such localities. Further north, from Cundinamarca to Boyacá and southern Santander, there is a gradual but notable increase in yellow underparts saturation with increasing latitude, which peaks in Serranía de las Quinchas (dpto. Boyacá) and the Virolín region (dpto. Santander) (Figs. 1J, 2). North of Virolín, underparts become less intensely yellow in the Yariguíes Mountains and Bucaramanga region. From Bucaramanga north to the Perijá range in Cesar, specimens show little further variation. *B. t. auricularis* is the senior name for east slope and East Andes populations. *B. t. baezae* would be treated as consubspecific with *auricularis* using concepts that require diagnosability or do not recognise points on a cline (e.g. Remsen 2010).

In the Central Andes, specimens and photographs of birds from near the head of the Magdalena Valley in dpto. Huila, in the south of this range, are similar to east-slope birds. More yellowish underparts on average occur in photographed birds from dpto. Tolima (Fig. 1G–H) and specimens from dptos. Valle del Cauca and Quindío (Fig. 2). There is no material available at c.02–04°N on the east slope of the Central Andes. Birds in Antioquia and San Lucas have the brightest yellow underparts, these being apparently indistinguishable morphologically. Gutiérrez-Pinto *et al.* (2012) drew attention to similarities between the San Lucas and northern Central Cordillera specimens, but considered them ‘phenotypically distinct’, citing Salaman *et al.* (2002) and Curson (2010). However, Salaman *et al.* (2002) had no northern Central Andes specimens available for direct comparison¹ and Curson (2010) based his summary on the literature.

It is not currently known if variation in underparts coloration in the Central Andes is clinal or step-clinal owing to the lack of material from southern Antioquia and Caldas (though USNM 436890, 427320 from Hacienda Sofia, río Samaná, are not as intensely yellow as those from Frijolera). The attainment of brighter yellow underparts occurs at similar latitudes to the East Andes cline.

Morphological similarities among birds from Virolín / Quinchas (East Andes) and the northern Central Andes resulted in a hypothesis (reflected, for example, in Donegan & Huertas 2005) that an undescribed subspecies with an upper Magdalena distribution on both Andean slopes could be involved. The subspecies limits suggested by Fjeldså & Krabbe (1990) and Curson (2010) may have been based on a similar understanding. However, specimens and mist-net captures from Serranía de los Yariguíes and Perijá, the nearest localities in the East Andes to Anorí and San Lucas, have duller underparts.

Peruvian and Bolivian Andes.—Plumage variation was discussed by Hellmayr (1935), Zimmer (1949), Fjeldså & Krabbe (1990), Curson *et al.* (1994) and Gutiérrez-Pinto *et al.* (2012). The nominate subspecies is generally treated as occurring over most of Peru. Fjeldså & Krabbe (1990) and Schulenberg *et al.* (2007) considered morphologically different birds (attributed to *B. t. inconspicuus*) to occur only in Puno in southernmost Peru. Curson *et al.* (1994) and Fjeldså & Krabbe (1990) thought that specimens from this region intergrade with Bolivian forms such as *punctipectus*, raising doubts as to the validity of the latter. However, there are no known intermediates between the *tristriatus* and *inconspicuus* groups in Puno.

¹ No *B. tristriatus* were reported by Salaman *et al.* (1999a) from the northern Central Andes. The earliest modern specimens from the Anorí region are dated 2002, based on Cuervo *et al.* (2008). At the time of their collection, Salaman *et al.* (2002) had already been submitted for publication.



Figure 2. ICN series showing underparts coloration of Three-striped Warbler *Basileuterus tristriatus* in Colombia. Top row, left: West Andes (*daedalus*, south to north, from left to right): Nariño (5), Cauca (1), Valle del Cauca (6), Antioquia (1). Top row, right: Tacarcuna (*tacarcunae*): Chocó (1). Second row: Head of Magdalena Valley (*auricularis*): Huila (1). Central Andes (*daedalus*, south to north from left to right): Quindío (4), Antioquia (10). San Lucas (subsp.) Bolívar (2). Bottom two rows: East Andes (*auricularis*, south to north from bottom to top and left to right). From bottom row: Cauca (1), Meta (1), Cundinamarca (4), Boyacá (Pajarito: 4; Cusiana: 5); second from bottom row: Boyacá (Quinchas: 1), Santander (Virolín: 5, Bucaramanga: 5, Surata: 1, Yariguíes: 2), Cesar / Perijá (5) (T. M. Donegan)

Biometric data

No population of *B. tristriatus* reaches even Level 2 (50%) diagnosability (Donegan (2008) for any biometric variable when compared with any other population, using any of the three biometric datasets (all specimens, males, mist-net data). Only *B. basilicus* of Santa Marta shows notable deviation from other populations in its biometrics, satisfying the Level 5 test of statistical diagnosability for tail length vis-à-vis *baezae* and *tacarcunae* based on the

dataset of all specimens. It also met the Level 2 (50% diagnosability) test from all *tristriatus* populations in tail length based on all data and from some of them in tarsus length based on all specimens and only males.

Vocal differences between *B. tristriatus* and other species

Two populations considered to be related to *B. tristriatus* by previous authors—namely Santa Marta Warbler *B. basilicus* and Three-banded Warbler *B. trifasciatus*—as well as two populations of *B. tristriatus* (*B. t. melanotis* including *chitreusis* and tentatively *B. t. tacarcunae* of Central America) differ in their vocalisations from other populations. The main song of *B. basilicus* (Fig. 6A–B) is broadly equivalent to ‘slow song’ of *tristriatus*. However, it is delivered as an incessant series of up to 200+ notes, not in short bursts. Moreover, the notes tend to be complex and long, often including multiple ‘turning points’. In the quantitative analysis, max. acoustic frequency was diagnosable from most (but not all) other populations, whilst number of notes, song length and min. acoustic frequency displayed substantial but usually not diagnosable (generally Level 2) differentiation. A brief playback study in Santa Marta using the recording in Fig. 6A revealed an aggressive territorial response (Fig. 6B), suggesting that this song is given by males. In contrast, the equivalent ‘slow song’ appears to be given by females in *B. tristriatus*. Simultaneous with the presumed male song, another individual (presumably female) often duets with a call comprising equally incessant, up-down strokes whose undertone generally is below male song and overtone above it (Fig. 6C). No equivalent type of vocalisation or such closely coordinated duetting occurs in any other populations studied here. Calls of *B. basilicus* (Fig. 7A) are also higher in frequency and of longer duration than *B. tristriatus* (Fig. 7C–N), being more distinct than those of Golden-crowned Warbler *B. culicivorus* (Fig. 7Q), which is often sympatric with *B. tristriatus* in Colombia. These vocal differences support species rank for *B. basilicus*.

The song of *B. trifasciatus* was considered by Ridgely & Greenfield (2001) to be ‘similar’ to that of *B. tristriatus*. This is borne out by quantitative study, which revealed no significant differences. However, rising song differs structurally in not including any appreciable initial trill (Fig. 4K–L). Venezuelan populations (Fig. 5 C–D) and some Peruvian recordings (Fig. 4G) approach *B. trifasciatus* in lacking a strong or long initial trill to rising song, but always include at least a small number of simple notes that increase in acoustic frequency. Slow song of *B. trifasciatus* is structurally different from all *B. tristriatus*. Although the coordinated duets of *B. basilicus* do not occur, note shape is closer to *B. basilicus*, comprising repeated up-down strokes of broad bandwidth (Fig. 7P), often interspersed with calls.

Ridgely & Greenfield (2001) queried whether *B. tristriatus* and *B. trifasciatus* might overlap in southern Ecuador. A recording identified as *B. tristriatus* from Azuay (ML82620), where *B. tristriatus* occurs, is typical of *B. trifasciatus* in its structure and all variables except song speed (15.5 notes / second vs. 7.6–13.7 for 47 *trifasciatus*). This recording could represent geographical variation and a northernmost record. Notably, the southern (nominate) subspecies has on average slower song. Alternatively, the recording may be of an individual intermediate between *B. trifasciatus* and *B. tristriatus daedalus* (the song speed of which averages 16.9 notes / second for trills (11.1–19.7) or 13.2 notes / second for scratchy notes (8.7–17.9). Further investigation is required into this potential contact zone.

Vocal variation in *B. tristriatus*

Central America.—Central American *B. t. melanotis* and *chitreusis* give rapid jumbled notes (Figs. 6D–F) equivalent structurally to the slow song of other populations. Call notes are also given (Fig. 7B). However, no rising song occurs in any Central American recording,

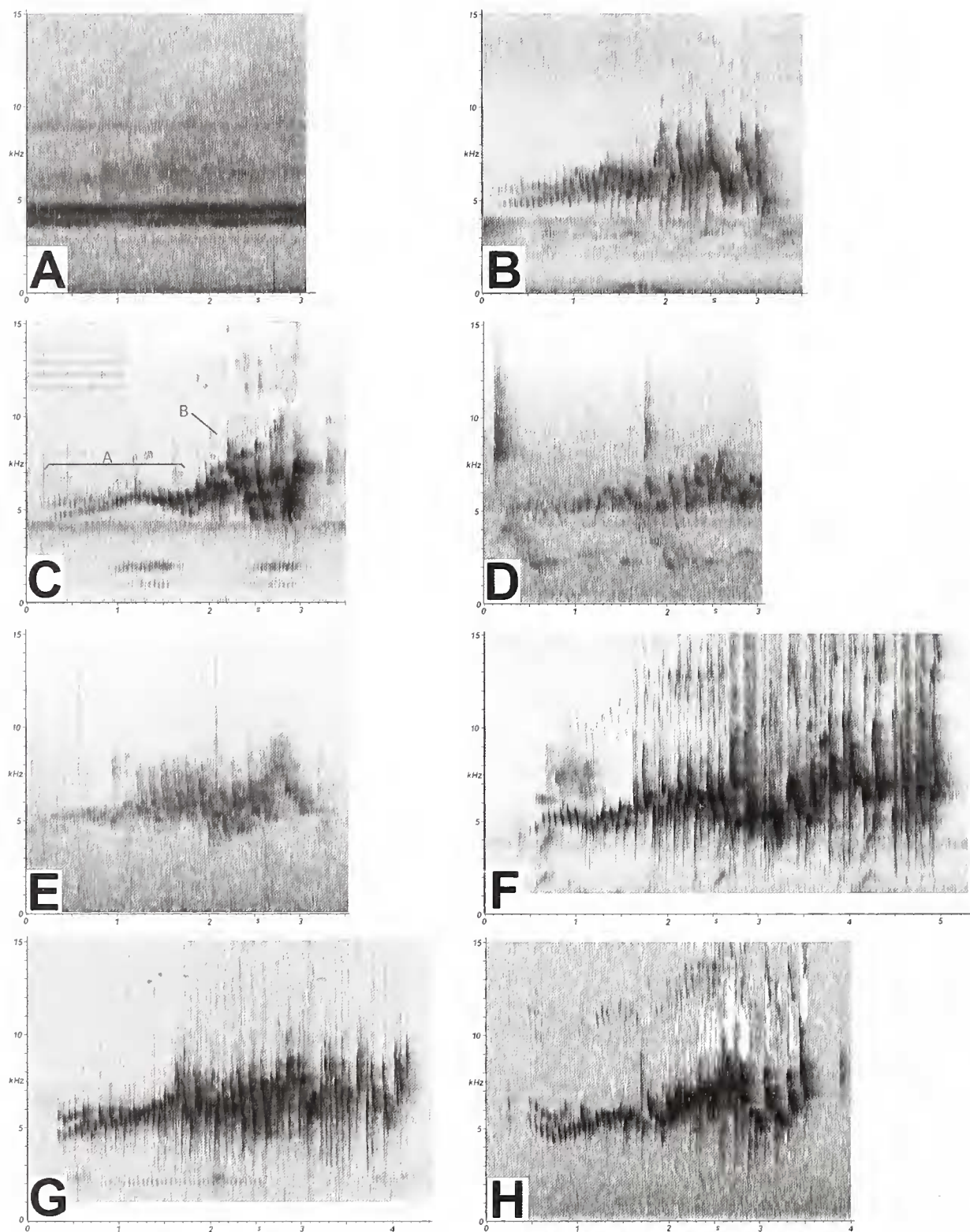


Figure 3. Rising songs of West and Central Andes and west slope populations. San Lucas, Colombia (subsp.): A. Santa Cecilia, Serranía de San Lucas (XC176120: T. M. Donegan). Central Andes, Colombia (*daedalus*): B. Hacienda Termópilas, El Laurel, Neira, Caldas (IAVH 7979: M. Álvarez). C. La Romera, Medellín, Antioquia (Boesman 2012: 3197-4). D. Reserva La Forzosa, Anorí, Antioquia (XC55260: B. López-Lanús). E. Reserva Bremen, Buenavista, Quindío (IAVH 7293: M. Álvarez). West Andes, Colombia (*daedalus*): F. El 18, Valle del Cauca (XC22420: A. Spencer). West slope (*daedalus*): G. Ricaurte, Reserva Natural La Planada, Nariño, Colombia (Álvarez *et al.* 2007, disc 7: 51a). H. Tandayapa Lodge, Pichincha, Ecuador (XC6717: N. Athanas). Sections 'A' and 'B' on 3C denote the 'trill' and 'scratchy' parts, respectively, of the rising song.

suggesting a different vocal repertoire. The song is faster than slow song of any other *B. tristriatus* population, with no overlap and statistical diagnosability from all populations (except *tacarcunae*, for which sample size was small). Songs are also higher pitched on average.

B. t. tacarcunae (of north-westernmost Colombia and southern / eastern Panama) has a different song. The single recording is incessant and scratchy. Although subdivided into two for analyses due to a small break, the sole recording could be considered *c.*300 notes long, greatly exceeding the number of notes and length in any other *B. tristriatus* population. It also has some more complex notes than those in other populations, with low churrs interspersed (Fig. 6G). It is closer to the male song of *B. basilicus* in length and structure than to *B. tristriatus*. However, the song is faster and higher pitched than the former. No other vocalisations are known.

Venezuela.—Recordings from the Mérida Andes and Coastal Cordillera are cohesive but show considerable intra-population variation (Fig. 5A–D). Notably, the distinction between slow and fast songs is less marked than in other Andean populations, with all being similarly (slow) paced with just a few short notes introducing rising songs, which can be considered equivalent to an opening trill. Rising song speed does not change dramatically between the trill and scratchy part. There are notable structural similarities to the rising song of *B. trifasciatus*, which shares a grey ground colour to its head. Songs have variable note shapes, sometimes principally characterised by long downstrokes (e.g. XC65916). Recordings of both song types also often include a falling cadence—a sequence of notes of progressively lower acoustic frequency—towards their middle (Fig. 5A–C), although in rising songs (Fig. 5D) this is weaker. Such cadences occur rarely in some other populations (e.g. XC112289: west Andes of Ecuador) and primarily characterise slow song in Bolivian populations, but are rare in nearby populations. In the quantitative analysis, rising song was found to have diagnosably slower opening trills than nearby East Andes (and various other) populations and significantly slower scratches.

Recordings of rising songs from Tamá National Park (Fig. 4A) are typical of faster-paced East Andes and east-slope recordings, confirming that vocalisations described for Venezuela are restricted to populations north and east of the Tachirá depression. *B. t. auricularis* has been listed for south-west Venezuela (e.g. Fjeldså & Krabbe 1990, Dickinson 2003) and Táchira (Hilty 2003, Restall *et al.* 2006) but only occurs on Tamá (and presumably Perijá) in this country.

No recordings are available from the Paria Peninsula or mountains of Sucre, which support vocally distinctive populations of other species (e.g. Donegan 2008). *B. tristriatus* there is only mildly differentiated in plumage from those in the Coastal Cordillera (Curson *et al.* 1994) and is considered close to other Venezuelan populations (Gutiérrez-Pinto *et al.* 2012).

Northern Andes.—*B. tristriatus* throughout most of the rest of the Andes to southern Peru is vocally fairly uniform, with all populations giving all three vocalisations discussed in the Methods (Figs. 4–5, 7). However, there are some notable differences in quantitative variables. Despite the plumage variation observed in the Colombian East Andes and east slope south to northern Peru, all rising songs, slow songs and calls from this broad region are similar (e.g. Figs. 4A–G, 5I–K, 7J–K). Rising songs in the East Andes usually have faster trills (Level 2) than Central and West Andes populations. The two last-named populations are vocally quite similar, with only small statistically significant differences in a few characters.

Slow song is more or less consistent in quantitative variables throughout the East Andes and east slope south to the Huancabamba depression, with individual notes

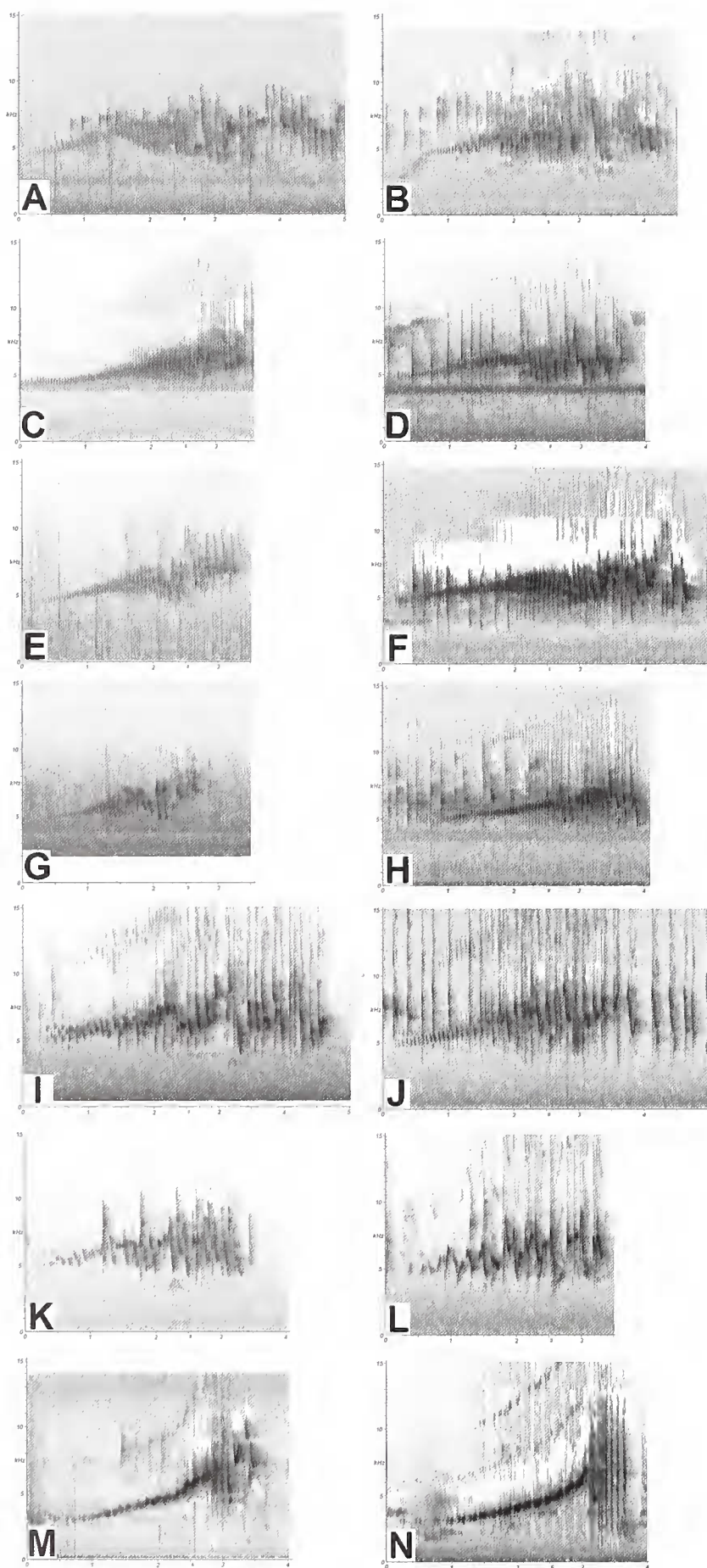


Figure 4. Rising songs of East Andes, east slope and southern populations. Colombia (*auricularis*): A. Sisavita, Carrizal, Cucutilla, Norte de Santander (IAVH 9098: S. Córdoba; also includes calls at start and slow song of second individual towards end). B. La Aurora, above Galán, Serranía de los Yariguíes, Santander (XC25502: T. M. Donegan). C. Medina, Cundinamarca (ML80874: M. Álvarez). D. PNN Los Picachos, Finca Andalucía, Caquetá (ML89242: M. Álvarez). E. PNN Cueva de los Guácharos, Acevedo, Huila (IAVH 7057: M. Álvarez). Ecuador ('*baezae*'): F. Cordillera Guacamayos, Napo (Krabbe & Nilsson 2003: 31-7). Peru north of Huancabamba depression ('*baezae*'): G. East slope of Cerro Chinguela, Lucuma, Cajamarca (ML21713: T. A. Parker). Peru south of Huancabamba depression (*tristriatus*): H. 15 km north-east of Jirillo, San Martín (ML42070: T. S. Schulenberg). I. Below Calabazas, Junín (ML147187: M. B. Robbins). Peru south of Apurímac (subsp.): J. San Pedro, south-west of Pilcopata on Cosñipata Highway, Cusco (ML85067: A. J. Begazo; also includes calls of second individual). West slope of Andes in southern Ecuador (*B. trifasciatus nitidior*): K. Loja, El Cisne-Ambocas road, Ecuador (XC81322: L. Ordóñez-Delgado). West slope of Andes in northern Peru (*B. t. trifasciatus*) L. Bosque Cachil, Cajamarca (XC75966: C. J. Schmitt). Bolivian Andes: M. Urpuma, Sandillani, Cotapata NP, La Paz (XC44438: T. M. Donegan). N. Miguelito, Cochabamba (XC1623: S. Mayer).

appearing rather vertical in sonograms (Fig. 5I–K). Recordings from San Lucas and the West and Central Andes and the west slope are similar quantitatively but all include some notes with a more slanted shape (Fig. 5E–H). The two available recordings of rising song in San Lucas are from the same bird. One is faint and distant but permits analysis (Fig. 3A), whilst in the second only a few variables could be measured. A short trill, early higher note and the sequence of individual scratchy notes thereafter are visible on the sonogram and audible when the volume is increased. These are generally similar to some Central Andes populations (Fig. 3B–D). However, the initial trill has fewer notes than any *B. tristriatus* recording from Colombia, Ecuador or Peru and is shorter than all except the shortest west Ecuadorian recording. The min. frequency of the scratchy part in both San Lucas rising songs is higher than in any Central or West Andes recording ($n = 67$). Without a larger sample, it is impossible to ascertain the extent to which apparent differences are diagnosable, but the lack of any overlap indicates differentiation. Moreover, slow songs in San Lucas (Fig. 5E) also fail to attain such low min. acoustic frequencies as nearby populations. Call notes (Fig. 7E–F) in San Lucas are similar to those of Central and West Andes and west-slope birds (Figs. 5F–H, 7G–I).

In conclusion, the pattern of vocal variation is not always consistent with morphology. West Andes and west-slope populations share vocalisations with Central Andean birds; the morphologically similar Central and East Andes populations differ vocally; no notable vocal variation tracks the dramatic north–south plumage clines in the Central or East Andes or in eastern Ecuador; and San Lucas birds, which are morphologically similar to those in the northern Central Andes, appear to show small vocal differences.

Peruvian Andes.—*B. tristriatus* occurs only on the east slope in Peru (Schulenberg *et al.* 2007), with *B. trifasciatus* replacing it in the west. A rising song from north of the Huancabamba depression (Cajamarca) is essentially identical to Colombian and Ecuadorian east-slope recordings (Fig. 4G). South of the Huancabamba depression to Bolivia rising songs are rather variable (Fig. 4H–J). Quantitative data are similar in northern Peru to eastern Ecuador and Colombia. In contrast, either side of the Apurímac Valley, proposed as a barrier by Gutiérrez-Pinto *et al.* (2012), there is significant but non-diagnosable variation in the speed of scratches and more minor but significant variation in other quantitative variables. Data indicate the presence of two different subspecies in this region of Peru. However, the two northernmost recordings (Boesman 1809-1 and ML42070) from south of the Huancabamba depression attain speeds of >16 notes / second and the slowest ‘northern’ recording (ML147187 at c.10–12 notes / second) is the southernmost of this sample, so clinal variation cannot be discounted without more extensive sampling and additional analyses.

Slow songs throughout most of Peru also differ from those north of the Huancabamba depression, with more slanted note shapes re-appearing (akin to slow song in the Central and West Andes and west slope: Fig. 5L–M). However, quantitative variables for this vocalisation are similar to northern populations and show no major differences within Peru.

Bolivia.—*B. tristriatus* throughout Bolivia (including the ranges of *B. t. punctipectus* and *canens*) possess a strikingly different rising song (Fig. 4M–N) to that in all recordings of this vocalisation north of the border (*cf.* Fig. 4I–J). Bolivian rising songs start with lower pitched notes than any other population, being fully diagnosable (Level 5) from all other *B. tristriatus* populations with sample size of more than two. The trill is also diagnosably slower than in all other populations except Venezuela and the Colombian Central Andes. Some recordings include very rapid scratchy notes at the end (Fig. 4N) but most have only a few scratchy notes, with fewer notes on average (Level 2 vs. most). Slow song also differs from most Andes populations in always including (and usually solely comprising)

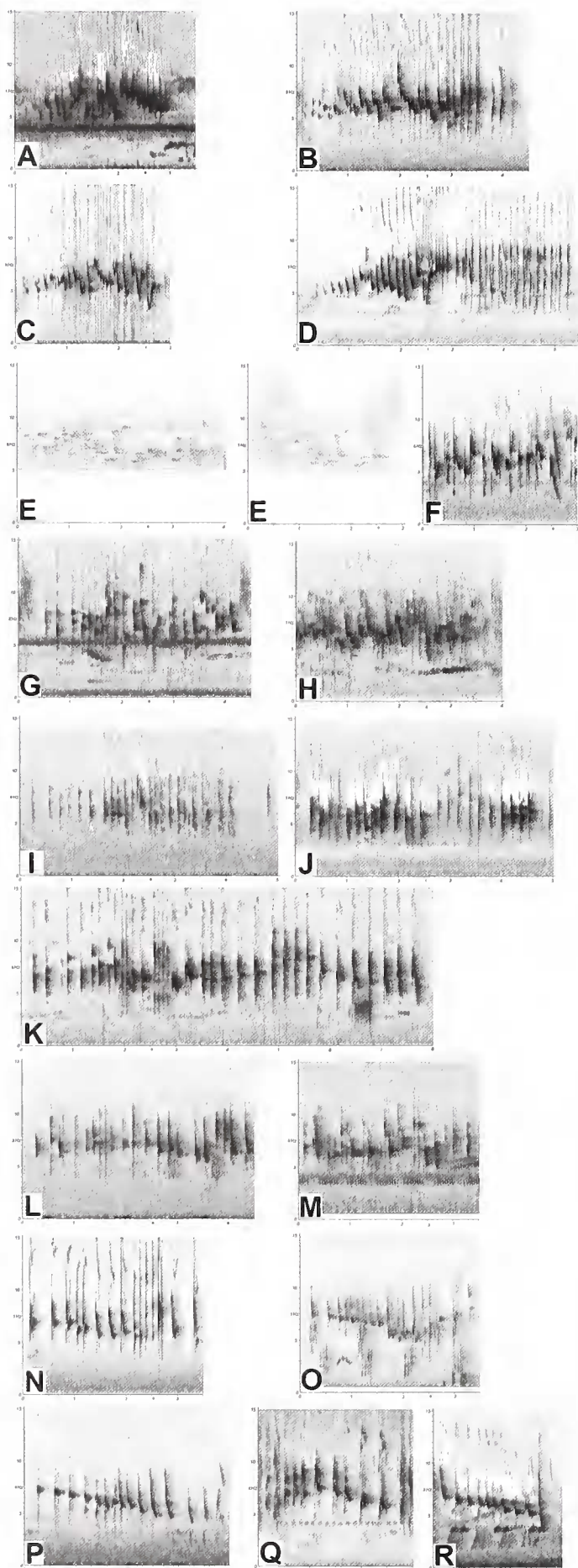


Figure 5. Songs from Venezuela and slow songs of other taxa. Coastal Cordillera, Venezuela (*bessereri*): A. Oripoto, Miranda (ML67198: P. A. Schwartz). B. Colonia Tovar, Aragua (ML53618: L. R. Macaulay). Andes of Venezuela (*meridanus*): C. PN Yacambú, Lara (Boesman 1999: 25-1). D. San Isidro quarry, Barinas (XC65916: D. F. Lane). San Lucas, Colombia (subsp.): E. Santa Cecilia, Serranía de San Lucas (XC176120: T. M. Donegan). Central Andes, Colombia (*daedalus*): F. Amalfi, Antioquia (Álvarez *et al.* 2007, disc 7: 51d). West Andes, Colombia (*daedalus*): G. rio Anchicayá, Valle del Cauca (ML83777: S. L. Hilty). West slope, Ecuador (*daedalus*): H. Tandayapa, Pichincha (XC6639: N. Athanas). East Andes, Colombia (*auricularis*): I. La Aurora, above Galán, Serranía de los Yariquíes, Santander (XC25502: T. M. Donegan). East slope, Ecuador ('*baezae*'): J. Cordillera Guacamayos, Napo (Krabbe & Nilsson 2003: 31-7). Peru south of Huancabamba depression (*tristriatus*): K. Abra Patricia-Alto Nieva, San Martín (XC20772: N. Athanas). L. North-east of Tingo María, Loreto (ML28805: A. B. van den Berg). M. 15 km north-east of Jirillo, San Martín (ML42070: T. S. Schulenberg). Peru south of Apurímac (subsp.): N. San Pedro, south-west of Pilcopata on Cosñipata highway, Cusco (ML85067: A. J. Begazo). O. Capiri, Marcapata, Cusco (XC22826: D. Geale). Bolivia (*punctipectus* group): P. Tokoaque, Madidi NP, La Paz (ML121704: A. B. Hennessey). Q. Urpuma, Sandillani, Cotapata NP, La Paz (XC44213: T. M. Donegan). R. Miguelito, Cochabamba (XC1623: S. Mayer).

falling cadences or series of consecutively lower notes (Fig. 5P–R), instead of the jumbled frequency of other populations.

The northern limit of birds with the Bolivian vocal type is unknown. Recent field work in Puno did not produce recordings of rising songs (Robbins *et al.* 2013). No Peruvian rising songs, including examples from the east slope of Cusco (Fig. 4J), approach those of Bolivian birds. However, two recordings of slow song in Cusco (Fig. 5N–O) and one from Puno exhibit unusual note shapes and include falling cadences, like Bolivian recordings. The type locality of *inconspicuus* (considered related to *punctipectus* of Bolivia on account of its morphology by Zimmer 1949) is in Puno, who considered the Urubamba Valley to separate the two groups.

Comparison with molecular data

Gutiérrez-Pinto *et al.* (2012) discussed how their molecular findings were consistent or incongruent with morphological variation. Additional comparisons are now possible including with vocal data.

The molecular and vocal data show some remarkable consistencies. In particular, the most vocally distinctive populations include *basilicus* of Santa Marta, *trifasciatus* of western Peru, *melanotis* of Costa Rica, *tacarcunae* of Panama / Colombia, and Bolivian populations (*punctipectus* group), which coincide with the deepest branches in the molecular phylogeny. Moreover, Gutiérrez-Pinto *et al.* (2012) found *B. basilicus* to be so distantly related as not to be congeneric with *B. tristriatus*. The lack of vocal differentiation along plumage clines in the Central and East Andes is consistent with these birds being more closely related to one another than to populations in other ranges. Moderate differences between the voice of Central and East Andes populations reflects near-monophyletic groups recovered in the molecular phylogeny. Finally, small vocal differences between San Lucas and other Colombian Andean populations, and those either side of the Apurímac in Peru, also reflect the phylogeny.

The molecular phylogeny has west-slope and West Andes populations embedded with those of the Central Andes, which is consistent with their vocal similarities. Most specimens are easily assigned to one population, but a small number of birds whose phenotype is like that of birds from the Central Andes in the Colombian West Andes suggests limited contact.

Some inconsistencies between vocal or morphological and molecular data merit discussion. Most notably, the vocally and morphologically divergent Venezuelan populations represent a relatively young branch of the molecular phylogeny. Another potential point of inconsistency is the unimpressive quantitative vocal differentiation between populations either side of the Marañón or Huancabamba depression in Peru. Specimens from south of the proposed Urubamba Valley divide for subspecies *inconspicuus* (Zimmer 1949) clustered with more northern populations assigned to *tristriatus*. Finally, *tacarcunae* and *trifasciatus* were sister taxa in the phylogeny, but resemble one another little in voice or plumage. Results of mitochondrial and nuclear DNA are often congruent (Zink & Barrowclough 2005) but anomalies may result from differing male and female dispersion rates (Peters *et al.* 2012), including in Parulidae (Gibbs *et al.* 2000). Alternatively, it has been suggested that peripheral populations can differentiate more quickly in vocal characters (Lara *et al.* 2012).

Species limits

Although my core aim was to address subspecific limits of *B. tristriatus* in Colombia, an unprecedented set of materials relevant to species limits was collated. Voice has been widely used to delimit species in suboscine passerines (in which vocalisations are considered

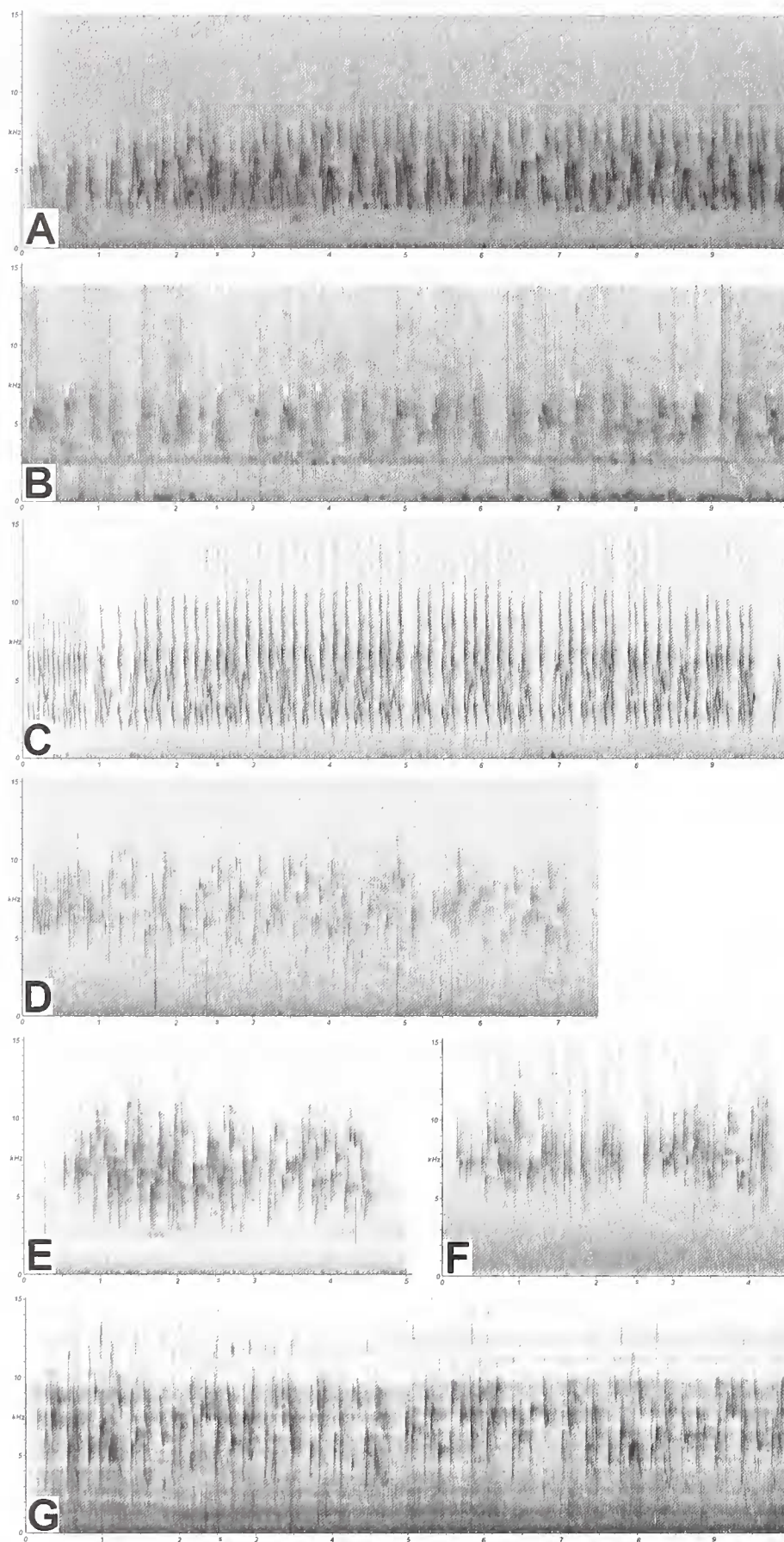


Figure 6. Vocally different populations from most Three-striped Warbler *Basileuterus tristriatus*. Santa Marta Warbler *B. basilicus*: A. RNA El Dorado or San Lorenzo ridge, Santa Marta, Magdalena, Colombia (Krabbe 2008, disc 2: 62). B. Idem (XC43566: T. M. Donegan). C. Idem, duet (XC117717: M. Álvarez). Costa Rica (*melanotis*): D. 90 km north-west of San José, Monteverde, Puntarenas (ML32713: L. F. Kibler). E. Monteverde Cloudforest Preserve, Guanacaste (ML32284: T. A. Parker). Eastern Panama (*chitrensis*): F. Cerro Colorado, Comarca Ngöbe-Bugle (XC145616: W. Adsett). Panama (*tacarcunae*): G. Chagres National Park, Panama (XC145623: W. Adsett).

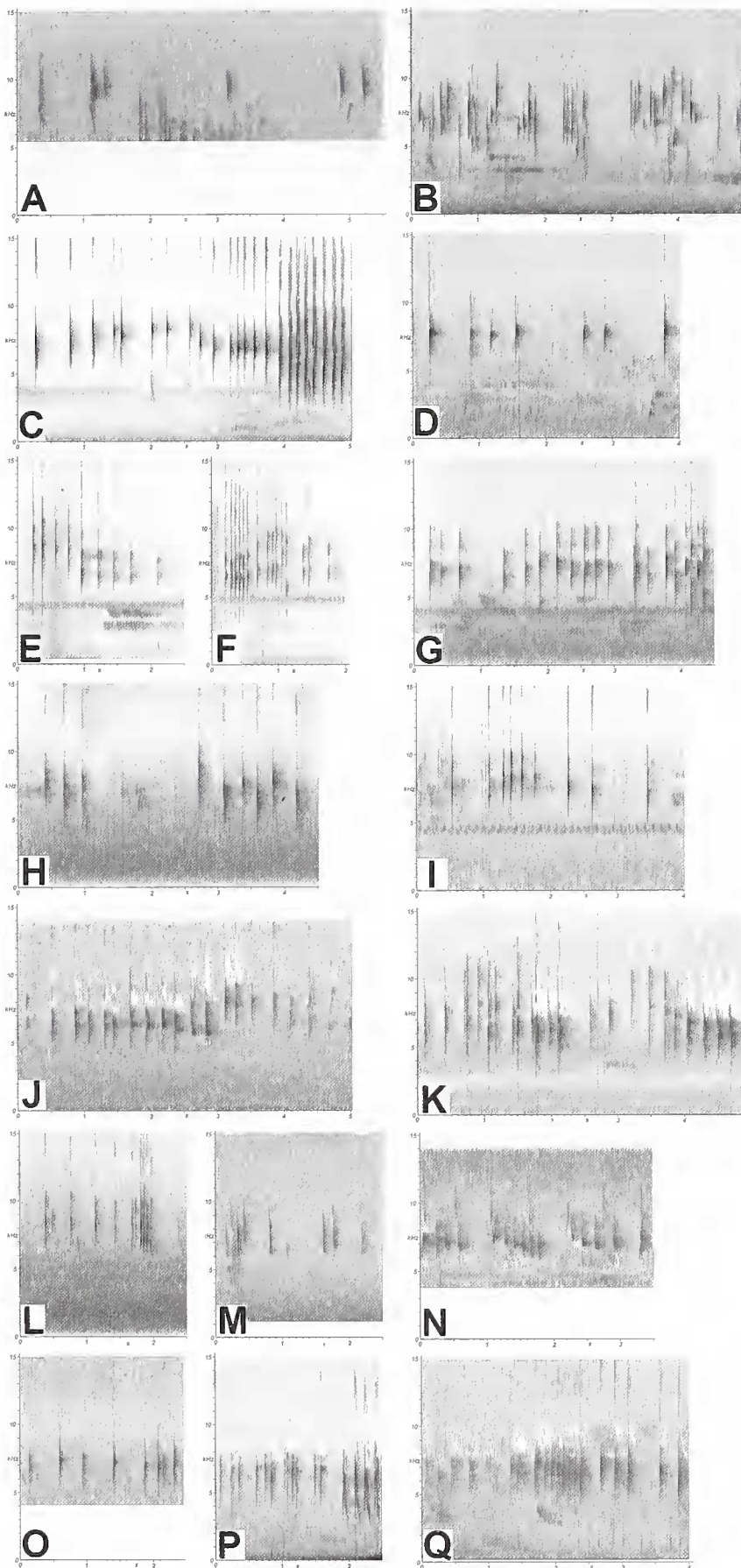


Figure 7. Calls. Santa Marta Warbler *Basileuterus basilicus*: A. RNA El Dorado or San Lorenzo ridge, Santa Marta, Magdalena, Colombia (Krabbe 2008, disc 2: 62). Costa Rica (*melanotis*): B. Monteverde Cloudforest Preserve, Guanacaste (ML39207: T. A. Parker). Coastal Cordillera, Venezuela (*besseri*): C. PN El Ávila, Distrito Federal (ML127798: C. A. Marantz). Venezuelan Andes (*meridanus*): D. 13 km east of Santo Domingo, Barinas (ML52699: S. L. Hilty). San Lucas, Colombia (subsp.): E–F. Santa Cecilia, Serranía de San Lucas (XC172116, 172118: T. M. Donegan). Central Andes, Colombia (*daedalus*): G. Amalfi, Antioquia (Álvarez *et al.* 2007, disc 7: 51d). West Andes, Colombia (*daedalus*): H. El Cairo, Serranía de los Paraguas, Valle del Cauca (Álvarez *et al.* 2007, disc 7: 51b). West slope, Ecuador (*daedalus*): I. Reserva Maquipacuna, Pichincha (ML80985: D. Ross). East Andes, Colombia (*auricularis*): J. La Aurora, above Galán, Serranía de los Yariquies, Santander (XC25881: T. M. Donegan). East slope, Ecuador ('*baezae*'): K. Cordillera Guacamayos, Napo (Krabbe & Nilsson 2003: 31-7). Peru south of Huancabamba depression (*tristriatus*): L. 15 km north-east of Villa Rica, Pasco (XC105613: D. F. Lane). Peru south of Apurímac (subsp.): M. San Pedro, south-west of Pilcopata on Cosñipata highway, Cusco (ML85067: A. J. Begazo). Bolivia (*punctipectus* group): N. Urpuma, Sandillani, Cotapata NP, La Paz (XC442216: T. M. Donegan). Southern Ecuador (*B. trifasciatus nitidior*): O. Loja–Catamayo road, Loja (ML68185: P. Coopmans). P. Tierra Colorada, Loja (Krabbe & Nilsson 2003: 30.1), with last four notes an example of 'slow song'. Northern Colombia (Golden-crowned Warbler *B. culicivorus indignus*): Q. Agua de la Virgen, Ocaña, Norte de Santander (XC20538: T. M. Donegan).



Figure 8. Close-up extracts of two sequences of birds in Fig. 2 showing (left) five head of Magdalena Valley and Central Andes specimens from part of its distribution with duller underparts: Huila (ICN 37008) and Quindío (ICN 37296, 37295, 37301, 37298); right: five West Andes specimens from Cauca (ICN 37461) and Valle del Cauca (ICN 25840, 25881, 25875, 25873) and Antioquia (ICN 35684). Note darker and more olivaceous flanks of West Andes birds (T. M. Donegan)

innate: Kroodsma 1984, Isler *et al.* 1998), but is relatively little used for Neotropical oscines. Vocal differences are nonetheless evident between allopatric oscine populations (e.g. Cadena *et al.* 2007, Donegan & Avendaño 2010). Gape muscle strength and bill mass must influence the vocal repertoire of oscines, e.g. their ability to trill at given speeds or deliver notes of certain lengths or frequencies (e.g. Podos *et al.* 2004), and vocal differentiation is considered relevant to species limits in all birds (e.g. Helbig *et al.* 2002, Tobias *et al.* 2010).

It is unclear whether all vocal variables found here to be differentiated reflect physiological or innate differences between populations. For example, from this study it appears that most *B. tristriatus* populations avoid acoustic frequencies used by crickets, cicadas or other insects, by singing at a higher pitch. It is perhaps no coincidence that the 'highest frequency' population (in San Lucas) has some of the highest frequency insects (max. 4.9–6.1 kHz vs. 4.2–4.6 kHz for Central Andes populations in a sample of slow songs) or that the lowest frequency songs (in Bolivia) rarely have insect calls vocalising together (and when insect calls are present, the rising song 'crosses the insect line': ML132723). It is unclear whether differences in usage of low frequencies are learned / behavioural or innate. Other differences, in repertoire, song structure, song speed and max. frequencies (which are unconstrained by insects) are probably reflective of physiological or innate differences.

Gutiérrez-Pinto *et al.* (2012) recommended that, within *B. tristriatus*, three species could be recognised to maintain monophyly, i.e. *melanotis*, *tacarcunae* and *tristriatus*. They also proposed maintaining *B. trifasciatus* (which is embedded in the *tristriatus* tree) as a species. Geographical variation in vocalisations supports treating *melanotis* and *tacarcunae* as separate species from the rest of *B. tristriatus* given diagnosable, quantitative differences and differences in repertoire. The Bolivian population, for which *punctipectus* is the oldest name, emerges as another strong candidate for species rank based on voice and occupies the next most basal position in the phylogeny. These three forms (*melanotis*, *tacarcunae* and *punctipectus*) are mutually diagnosable and from remaining *tristriatus* in plumage.

Venezuelan populations are also quite distinctive in their rising song and dull plumage. However, splitting them would render *B. tristriatus* highly paraphyletic without broader

separation of Andean group members that display non-diagnosable vocal differences and more minor plumage differences.

Various geographical gaps in sound-recordings render novel arrangements provisional. In particular, *tacarcunae* and San Lucas rising songs are known from just one recording each, and there are no recordings of songs from the Paria Peninsula in Venezuela or Puno, Peru. Gutiérrez-Pinto *et al.* (2012) suggested that an 'integrative study of species delimitation ... including an expanded genetic sampling, as well as behavioral, phenotypic, and ecological information' is necessary before formally evaluating further changes to current taxonomy. The present paper does not address additional genetic sampling, behaviour (other than vocal) or ecology. However, with the near-contemporaneous publication of two detailed, independent studies, it seems appropriate to re-evaluate species limits. The following sequence is more consistent with vocal and plumage variation:

Costa Rican Warbler *B. melanotis* (including *B. m. chitrensis*).

Tacarcuna Warbler *B. tacarcunae* monotypic.

Three-striped Warbler *B. tristriatus* (including *B. t. pariae*, *bessereri*, *meridanus*, *auricularis*, *daedalus*, 'baezae' and the undescribed San Lucas and south Peruvian populations).

Bolivian Warbler *B. punctipectus* (including dubious *B. p. inconspicuus* and *canens*).

All meet the Tobias *et al.* (2010) scoring tests, acquiring at least six points for voice and two for plumage (typically more). The only exception is Bolivian with just four for voice, but it scores three for speckling on the breast and one for underparts coloration. Interaction between *B. trifasciatus* and *B. tristriatus* in southern Azuay, Ecuador, requires further research, but they appear to have maintained vocal, molecular and morphological differences despite potential for contact, so no change to present taxonomy is proposed.

Some populations emerge as high priorities for research and conservation. In particular, *B. (t.) tacarcunae* is a rare and apparently declining taxon with a tiny geographical range, at high elevations in eastern Panama and extreme north-west Colombia. It formerly occurred on the Cerro Jefe ridge above Cerro Azul (Ridgely & Gwynne 1989), but has not been seen there recently and is apparently absent from Cerro Pirre and other drier localities (K. Allaire & W. Adsett *in litt.* 2012). There are no records from Chucantí (M. Miller & G. Berguido *in litt.* 2012) but it should occur in more humid forest nearby. *B. (t.) tacarcunae* has been observed at Cerro Guagaral and Cerro Brewster (W. Adsett *in litt.* 2012) and was recently collected on the Colombian side of Cerro Tacarcuna (J. Avendaño pers. comm.; Fig. 1A). Conservation is currently complicated due to several of the few known localities for *tacarcunae* being threatened with habitat modification or coinciding with the Darién Gap, a region notoriously largely outside government control. Taxonomy should be based solely on relevant characters, but resolving the species limits discussed here could have practical implications for conservation.

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Appendix 1: Biometric data

Data presented as: mean \pm standard deviation (lowest value–highest recorded value) (n = no. of specimens or individuals). Live capture data from: *West Andes and west slope*: Reserva Natural Tambito, Cauca (L. M. Dávalos, TMD). Río Nambí, Nariño (P. Salaman); Reserva Natural de Aves (RNA) Eriocnemis, Cauca (L. F. Barrera, J. Sandoval / ProAves). RNA Pangan, Nariño (H. Arias / ProAves); RNA Jardín, Antioquia (G. Suárez / ProAves). *San Lucas*: La Punta, Bolívar (P. Salaman, A. Cuervo, TMD); Santa Cecilia, Bolívar (TMD). *Central Andes*: RNA Arrierito Antioqueño, Antioquia (C. Olaciregui, D. Velasco, A. Tovar / ProAves), La Floresta and Aguas Frías, Caldas (F. Guerrero / ProAves). Reserva Ibanasca, Tolima (A. González / ProAves). *East Andes*: Serranía de los Yariquíes, Santander: El Talismán, Honduras Alto, La Luchata, La Aurora, Cerro de la Paz (E. Briceño, J. Avendaño, B. Huertas, TMD); RNA Reinita Cerulea, Santander and RNA Pauxi pauxi, Santander (R. Parra, J. C. Luna / ProAves); Reserva Natural Cachalú, Santander (S. Vaillmarin, A. Daza. A. Magaly); Serranía de los Churumbelos, Cauca: Alto Cagadero and Nabú (P. Salaman, A. Cuervo, TMD). For coordinates and details of localities, see Donegan & Dávalos (1999), Donegan *et al.* (2007), Donegan (2012) and Salaman *et al.* (1999b, 2002, 2010).

Population	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Culmen to base of bill (mm)	Body mass (g)
SPECIMEN DATA					
<i>B. basilicus</i>	65.4 \pm 2.94 (61–70) (n = 7)	63.9 \pm 3.54 (58.5–69.4) (n = 7)	23.1 \pm 0.82 (22.2–24.3) (n = 7)	14.3 \pm 0.83 (13.2–15.4) (n = 7)	/
Males	69.0 \pm 1.41 (68–70) (n = 2)	68.0 \pm 2.05 (66.5–69.4) (n = 2)	24.2 \pm 0.21 (24.0–24.3) (n = 2)	14.1 \pm 1.27 (13.2–15.0) (n = 2)	/
Females	64.0 \pm 1.87 (61–66) (n = 5)	62.3 \pm 2.52 (58.5–65.2) (n = 5)	22.7 \pm 0.53 (22.2–23.5) (n = 5)	14.4 \pm 0.77 (13.3–15.4) (n = 5)	/
<i>B. melanotis</i>					
<i>B. m. melanotis</i> Costa Rica and westernmost Panama	60.53 \pm 2.68 (55.0–64.5) (n = 18)	51.69 \pm 1.90 (49–55) (n = 18)	21.11 \pm 1.12 (19.0–24.5) (n = 18)	12.47 \pm 0.67 (11.0–13.5) (n = 17)	/
Males	62.07 \pm 1.30 (61.0–64.5) (n = 7)	52.50 \pm 1.32 (51.0–55.0) (n = 7)	21.29 \pm 1.60 (19.5–24.5) (n = 7)	12.71 \pm 0.64 (11.5–13.5) (n = 7)	/
Females	57.5 \pm 2.07 (55–60) (n = 6)	50.50 \pm 1.52 (49–53) (n = 6)	20.75 \pm 0.88 (19.0–21.5) (n = 6)	12.08 \pm 0.74 (11–13) (n = 6)	/
<i>B. m. chitrensis</i> west Panama	59.29 \pm 2.59 (54.5–66.0) (n = 19)	50.85 \pm 2.36 (47–55) (n = 20)	21.15 \pm 1.04 (19–23) (n = 20)	12.88 \pm 0.53 (12.0–14.0) (n = 20)	/
Males	59.85 \pm 3.23 (54.5–66.0) (n = 10)	52.1 \pm 2.37 (48–55) (n = 10)	21.35 \pm 0.97 (19.5–22.5) (n = 10)	12.95 \pm 0.6 (12.0–13.5) (n = 10)	/
Females	58.57 \pm 1.72 (56–61) (n = 7)	49.88 \pm 1.55 (47–52) (n = 8)	20.94 \pm 1.27 (19–23) (n = 8)	12.81 \pm 0.53 (12.5–14.0) (n = 8)	/
<i>B. tacarcunae</i> east Panama & north-west Colombia	59.93 \pm 2.86 (56–64) (n = 14)	50.32 \pm 2.22 (47–54) (n = 14)	20.11 \pm 0.71 (19.0–21.5) (n = 14)	12.61 \pm 0.49 (11.5–13.5) (n = 14)	13.25 (n = 1)
Males	60.63 \pm 2.86 (57–64) (n = 8)	51.19 \pm 1.65 (48–53) (n = 8)	20.0 \pm 0.65 (19–21) (n = 8)	12.81 \pm 0.37 (12.5–13.5) (n = 8)	13.25 (n = 1)
Females	57.50 \pm 1.91 (56.0–60.0) (n = 4)	48.00 \pm 0.82 (47.0–49.0) (n = 4)	20.25 \pm 1.04 (19.0–21.5) (n = 4)	12.13 \pm 0.48 (11.5–12.5) (n = 4)	/
<i>B. tristriatus</i>					
<i>B. t. pariae</i> Paria Peninsula, Venezuela	58.67 \pm 2.52 (56–61) (n = 3)	53.33 \pm 2.52 (51–56) (n = 3)	20.33 \pm 0.29 (20.0–20.5) (n = 3)	12.5 \pm 0.50 (12–13) (n = 3)	/

Population	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Culmen to base of bill (mm)	Body mass (g)
Males	60.00 ± 1.41 (59–61) (<i>n</i> = 2)	54.50 ± 2.12 (53–56) (<i>n</i> = 2)	20.25 ± 0.35 (20.0–20.5) (<i>n</i> = 2)	12.25 ± 0.35 (12.0–12.5) (<i>n</i> = 2)	/
<i>B. t. meridanus</i> type Mérida Andes, Venezuela	63.0 (<i>n</i> = 1)	51.0 (<i>n</i> = 1)	20.0 (<i>n</i> = 1)	12.5 (<i>n</i> = 1)	/
<i>B. t.</i> subsp. Serranía de San Lucas, Colombia	60.0 ± 2.32 (59–61) (<i>n</i> = 2)	52.5 ± 0.71 (52–53) (<i>n</i> = 2)	19.3 ± 1.77 (18.0–20.5) (<i>n</i> = 2)	13.5 ± 0.00 (13.5) (<i>n</i> = 2)	13.0 ± 1.41 (12–14) (<i>n</i> = 2)
Male	61.0 (<i>n</i> = 1)	53.0 (<i>n</i> = 1)	20.5 (<i>n</i> = 1)	13.5 (<i>n</i> = 1)	14.0 (<i>n</i> = 1)
Female	59.0 (<i>n</i> = 1)	52.0 (<i>n</i> = 1)	18.0 (<i>n</i> = 1)	13.5 (<i>n</i> = 1)	12.0 (<i>n</i> = 1)
<i>B. t. daedalus</i> Central Andes, Colombia	62.07 ± 2.22 (59–66) (<i>n</i> = 15)	54.4 ± 2.16 (51–58) (<i>n</i> = 15)	21.1 ± 1.09 (19–23) (<i>n</i> = 15)	12.97 ± 0.35 (12.5–13.5) (<i>n</i> = 15)	13.15 ± 1.28 (10.5–15.5) (<i>n</i> = 15)
Males	62.82 ± 2.09 (60–66) (<i>n</i> = 11)	55.27 ± 1.79 (53–58) (<i>n</i> = 11)	21.41 ± 1.02 (20–23) (<i>n</i> = 11)	12.95 ± 0.35 (12.5–13.5) (<i>n</i> = 11)	13.35 ± 1.04 (12.0–15.5) (<i>n</i> = 11)
Females	60.33 ± 0.58 (60–61) (<i>n</i> = 3)	51.67 ± 0.58 (51–52) (<i>n</i> = 3)	20.17 ± 1.04 (19–21) (<i>n</i> = 3)	13.0 ± 0.5 (12.5–13.5) (<i>n</i> = 3)	11.83 ± 1.26 (10.5–13.0) (<i>n</i> = 3)
<i>B. t. daedalus</i> West Andes and west slope, Colombia & Ecuador	61.57 ± 3.48 (56–69) (<i>n</i> = 20)	51.55 ± 2.35 (47.0–55.0) (<i>n</i> = 20)	20.43 ± 0.93 (19.0–22.5) (<i>n</i> = 22)	12.82 ± 0.33 (12.0–13.5) (<i>n</i> = 23)	12.18 ± 1.18 (10.5–13.0) (<i>n</i> = 4)
Males	64.18 ± 2.64 (61–69) (<i>n</i> = 11)	52.70 ± 2.41 (48–55) (<i>n</i> = 10)	21.05 ± 0.76 (20.0–22.5) (<i>n</i> = 11)	12.91 ± 0.20 (12.5–13.0) (<i>n</i> = 11)	13.0 ± 0.00 (13.0) (<i>n</i> = 2)
Females	58.72 ± 1.92 (56–61) (<i>n</i> = 9)	50.63 ± 1.69 (47–52) (<i>n</i> = 8)	19.72 ± 0.67 (19.0–20.5) (<i>n</i> = 9)	12.72 ± 0.44 (12.0–13.5) (<i>n</i> = 9)	11.35 ± 1.20 (10.5–12.2) (<i>n</i> = 2)
<i>B. t. auricularis</i> East Andes, east slope and head of Magdalena Valley, Colombia	61.45 ± 2.77 (54–65) (<i>n</i> = 42)	54.29 ± 2.72 (47–60) (<i>n</i> = 41)	20.51 ± 0.83 (19–22) (<i>n</i> = 40)	12.56 ± 0.70 (10.5–14.0) (<i>n</i> = 42)	12.52 ± 1.61 (10–15) (<i>n</i> = 17)
Males	62.77 ± 1.47 (60–65) (<i>n</i> = 24)	55.38 ± 1.84 (52–60) (<i>n</i> = 24)	20.92 ± 0.75 (19.5–22.0) (<i>n</i> = 24)	12.83 ± 0.58 (11.5–14.0) (<i>n</i> = 24)	12.32 ± 1.50 (10.5–15.0) (<i>n</i> = 9)
Females	59.00 ± 2.65 (54–63) (<i>n</i> = 13)	53.38 ± 2.81 (49–58) (<i>n</i> = 13)	20.08 ± 0.64 (19.0–21.5) (<i>n</i> = 13)	12.46 ± 0.43 (11.5–13.0) (<i>n</i> = 13)	10.97 ± 0.79 (10–12) (<i>n</i> = 7)
<i>B. t. 'baezae'</i> east slope, Ecuador	63.80 ± 1.75 (62.0–65.5) (<i>n</i> = 5)	51.42 ± 1.02 (50–53) (<i>n</i> = 6)	20.17 ± 1.08 (18.5–21.5) (<i>n</i> = 6)	12.52 ± 0.58 (11.5–13.0) (<i>n</i> = 6)	/
Males	63.0 ± 1.41 (62–64) (<i>n</i> = 2)	50.75 ± 1.06 (50.0–51.5) (<i>n</i> = 2)	20.25 ± 1.06 (19.5–21.0) (<i>n</i> = 2)	12.75 ± 0.35 (12.5–13.0) (<i>n</i> = 2)	/
Female	65.5 (<i>n</i> = 1)	53.0 (<i>n</i> = 1)	20.0 (<i>n</i> = 1)	12.5 (<i>n</i> = 1)	/
<i>B. t. tristriatus</i> Peru	59.0 (<i>n</i> = 1)	53.0 (<i>n</i> = 1)	19.5 (<i>n</i> = 1)	12.0 (<i>n</i> = 1)	/
<i>B. punctipectus</i> group Bolivia	59.5 ± 2.12 (58–61) (<i>n</i> = 2)	55.0 (<i>n</i> = 1)	20.25 ± 0.35 (20.0–20.5) (<i>n</i> = 2)	12.25 ± 0.35 (12.0–12.5) (<i>n</i> = 2)	/

LIVE CAPTURE DATA

B. tristriatus

<i>B. t.</i> subsp. Serranía de San Lucas, Colombia	65.11 ± 3.10 (61–70) (<i>n</i> = 9)	54.80 ± 3.16 (49.0–60.7) (<i>n</i> = 9)	20.83 ± 0.95 (19.5–22.9) (<i>n</i> = 9)	12.31 ± 0.90 (10.2–13.4) (<i>n</i> = 9)	12.29 ± 0.83 (11.3–14.0) (<i>n</i> = 9)
<i>B. t. auricularis</i> East Andes and east slope, Colombia	63.79 ± 3.01 (58–71) (<i>n</i> = 84)	55.96 ± 3.25 (50.7–65.1) (<i>n</i> = 32)	20.53 ± 0.69 (19.5–22.4) (<i>n</i> = 35)	12.4 ± 0.77 (10.0–13.6) (<i>n</i> = 35)	12.86 ± 1.14 (10.7–16.5) (<i>n</i> = 79)

Population	Wing-chord (mm)	Tail (mm)	Tarsus (mm)	Culmen to base of bill (mm)	Body mass (g)
<i>B. t. daedalus</i> Central Andes, Colombia	62.08 ± 2.87 (56–66) (<i>n</i> = 30)	60.2 (<i>n</i> = 1)	20.0 (<i>n</i> = 1)	11.82 (<i>n</i> = 1)	12.80 ± 1.11 (10.9–14.9) (<i>n</i> = 26)
<i>B. t. daedalus</i> West Andes and west slope, Colombia	62.62 ± 3.09 (55–70) (<i>n</i> = 119)	51.50 ± 3.11 (47.7–56.6) (<i>n</i> = 9)	20.69 ± 0.96 (19.3–22.5) (<i>n</i> = 9)	/	13.02 ± 1.03 (10.3–15.5) (<i>n</i> = 150)

Appendix 2: Vocal data

For songs of *B. basilicus*, Central American populations and slow songs of Andean *B. tristriatus* taxa, the following variables were measured (with bracketed capitalised codes used in tables below): (i) number of notes in song (NN); (ii) total song duration (seconds) (SL); (iii) song speed (dividing i by ii) (SS); (iv) max. acoustic frequency of highest note (kHz) (MF); (v) min. acoustic frequency of lowest note (kHz) (mF); (vi) frequency variation (subtracting iv from v) (FV). For rising songs of Andean *B. tristriatus* and *B. trifasciatus*, song was considered to comprise two parts for analyses: (A) initial rising trill, from start of vocalisation until point at which either note shape first changes significantly following initial increase in frequency or point at which max. frequency ceases to increase or is broadly stable; and (B) subsequent ‘scratchy part’, starting at end of trill and ending at the vocalisation’s terminus. The following vocal variables were measured: (i) number of notes in trill (NNT); (ii) number of notes in scratchy part (NNS); (iii) duration of trill (seconds) (SLT); (iv) duration of scratchy part (seconds) (SLS); (v) total song duration (seconds) (SL); (vi) speed of trill (dividing i by iii) (SST); (vii) speed of scratchy part (dividing ii by iv) (SSS); (viii) max. acoustic frequency of lowest note in trill (kHz) (mFT); (ix) max. acoustic frequency of highest note in trill (kHz) (MFT); (x) frequency variation of trill (subtracting viii from ix) (FVT); (xi) min. acoustic frequency of lowest note in scratchy part (kHz) (mFS); (xii) max. acoustic frequency of highest note in scratchy part (kHz) (MFS). Frequency variation of scratchy part (subtracting xi from xii) was also measured in rising songs but data are not presented here as substantial overlap was found for most taxa. For rising songs of *B. trifasciatus*, no clear initial trill was evident although the first few notes are always lower pitched. For such vocalisations, a dataset was taken of ‘short songs’, plus variable (viii) as for rising songs (based on max. acoustic frequency of the lowest of first four notes). Data for such vocalisations are given alongside rising song data as if all notes were in scratchy part of songs. Calls were not measured for any taxon, nor were short fast trills sometimes given by northern *B. tristriatus* populations or non-comparable apparent female calls of *B. basilicus*.

As vocalisations sometimes included a combination of frequencies delivered simultaneously, all main (loud) tones were included. Harmonic overtones were ignored. Overtones at start of trills were often given but always ignored for purposes of determining mFT. Up to three different examples of each vocalisation type were measured from each recording. Recordings probably of same individual, even on different archived recordings, were treated together, with later recordings excluded from analyses. Additional recordings were ignored if involving consecutive or near-consecutive original tracks, or made within two hours by same recordist at same locality and if recordings had similar mensural variables. On most recordings, the first three vocalisations (where available) of each kind were analysed, but in some recordings if the individual approached closer permitting greater definition on sonograms, later recordings were used. In a handful of recordings with two individuals vocalising, additional datasets were taken per vocalisation type per individual. As many recordings from as many localities as possible were included, to determine the full range of variables. All recordings under natural conditions and after playback were included. The highest- and lowest-recorded values for each variable for each vocalisation for each taxon were double-checked. Songs of *B. basilicus* and Central American taxa were only compared with the structurally most similar slow songs of other *B. tristriatus* (notwithstanding the different sexes that appear to give relevant vocalisations) as a conservative approach to assess differentiation. Various tests were applied to pairs of vocal and biometric variables to assess if postulated statistical tests considered relevant to species or subspecies rank had been passed, following Donegan (2008, 2012). Vocal data from applying these methods are as follows.

Songs of *B. basilicus* and Central American populations.

Taxon	NN	SL (s)	SS (notes/s)	mF (kHz)	MF (kHz)	FV (kHz)
<i>B. basilicus</i> Santa Marta, Colombia (<i>n</i> _{at} = 7)	125.22 ± 59.06 (63–267) (<i>n</i> = 9)	30.52 ± 18.63 (18.62–76.83) (<i>n</i> = 9)	4.34 ± 1.03 (3.20–5.98) (<i>n</i> = 9)	1.70 ± 0.52 (0.54–2.30) (<i>n</i> = 9)	7.67 ± 0.34 (6.97–8.08) (<i>n</i> = 9)	5.97 ± 0.67 (5.29–7.49) (<i>n</i> = 9)
<i>B. m. melanotis</i> Costa Rica (<i>n</i> _{at} = 7)	30.87 ± 16.77 (7–56) (<i>n</i> = 16)	2.20 ± 1.33 (0.40–4.01) (<i>n</i> = 16)	14.86 ± 1.75 (12.76–17.56) (<i>n</i> = 16)	3.18 ± 0.69 (2.28–4.35) (<i>n</i> = 16)	11.91 ± 0.69 (10.67–13.26) (<i>n</i> = 16)	8.73 ± 1.05 (7.26–10.42) (<i>n</i> = 16)

<i>B. m. chitrensis</i>	31.67 ± 2.08	2.07 ± 0.39	15.63 ± 2.67	4.02 ± 0.51	13.05 ± 0.94	9.03 ± 0.75
Panama	(30–56)	(1.65–2.41)	(12.86–18.19)	(3.49–4.52)	(12.86–18.19)	(8.58–9.89)
(<i>n</i> _{ai} = 2)	(<i>n</i> = 3)	(<i>n</i> = 3)	(<i>n</i> = 3)	(<i>n</i> = 3)	(<i>n</i> = 3)	(<i>n</i> = 3)
<i>B. melanotis</i>	31.0 ± 15.32	2.18 ± 1.22	14.98 ± 1.86	3.31 ± 0.73	12.09 ± 0.82	8.78 ± 1.00
combined	(7–56)	(0.40–4.01)	(12.76–18.19)	(2.28–4.52)	(10.67–13.94)	(7.26–10.42)
(<i>n</i> _{ai} = 9)	(<i>n</i> = 19)	(<i>n</i> = 19)	(<i>n</i> = 19)	(<i>n</i> = 19)	(<i>n</i> = 19)	(<i>n</i> = 19)
<i>B. tacarcunae</i>	164.0 ± 26.87	21.22 ± 2.74	7.71 ± 0.27	2.22 ± 0.08	10.83 ± 0.12	8.61 ± 0.03
Panama	(145–183)	(19.28–23.15)	(7.52–7.90)	(2.16–2.28)	(10.74–10.92)	(8.58–8.64)
(<i>n</i> _{ai} = 1)	(<i>n</i> = 2)	(<i>n</i> = 2)	(<i>n</i> = 2)	(<i>n</i> = 2)	(<i>n</i> = 2)	(<i>n</i> = 2)
Slow songs						
Taxon	NN	SL (s)	SS (notes/s)	mF (kHz)	MF (kHz)	FV (kHz)
<i>B. t. bessereri</i>	26.2 ± 26.37	3.23 ± 3.36	8.39 ± 0.74	3.02 ± 0.25	11.44 ± 1.32	8.42 ± 1.46
Coastal Cordillera,	(12–73)	(1.30–9.16)	(7.71–9.20)	(2.84–3.46)	(10.3–12.9)	(6.83–9.97)
Venezuela	(<i>n</i> = 5)	(<i>n</i> = 5)	(<i>n</i> = 5)	(<i>n</i> = 5)	(<i>n</i> = 5)	(<i>n</i> = 5)
(<i>n</i> _{ai} = 2)						
<i>B. t. meridanus</i>	17.71 ± 8.20	2.09 ± 1.01	8.56 ± 0.74	3.30 ± 0.43	10.32 ± 0.35	7.02 ± 0.70
Mérida, Venezuela	(6–31)	(0.78–3.70)	(7.67–10.06)	(2.76–3.99)	(9.85–10.98)	(6.27–8.22)
(<i>n</i> _{ai} = 4)	(<i>n</i> = 7)	(<i>n</i> = 7)	(<i>n</i> = 7)	(<i>n</i> = 7)	(<i>n</i> = 7)	(<i>n</i> = 7)
<i>B. t. subsp.</i>	14.5 ± 5.51	2.28 ± 1.10	6.64 ± 0.80	5.39 ± 0.32	9.94 ± 0.84	4.55 ± 1.15
San Lucas	(9–21)	(1.17–3.62)	(5.80–7.67)	(5.12–5.74)	(9.02–10.98)	(3.28–5.86)
(<i>n</i> _{ai} = 3)	(<i>n</i> = 4)	(<i>n</i> = 4)	(<i>n</i> = 4)	(<i>n</i> = 4)	(<i>n</i> = 4)	(<i>n</i> = 4)
<i>B. t. daedalus</i> Central	15.88 ± 10.63	2.26 ± 1.23	7.06 ± 1.23	3.98 ± 0.68	10.20 ± 0.80	6.32 ± 0.74
Andes	(8–62)	(0.80–7.26)	(5.41–10.06)	(1.78–4.72)	(8.79–11.93)	(4.97–7.66)
(<i>n</i> _{ai} = 16)	(<i>n</i> = 25)	(<i>n</i> = 28)	(<i>n</i> = 25)	(<i>n</i> = 25)	(<i>n</i> = 28)	(<i>n</i> = 5)
<i>B. t. daedalus</i> West	21.33 ± 10.44	3.21 ± 1.92	7.08 ± 1.62	3.68 ± 0.73	10.78 ± 0.66	7.12 ± 1.14
Andes, Colombia, and	(10–54)	(0.91–9.43)	(4.69–12.05)	(2.52–5.36)	(9.70–12.84)	(5.27–10.33)
west slope, Colombia	(<i>n</i> = 39)	(<i>n</i> = 39)	(<i>n</i> = 39)	(<i>n</i> = 38)	(<i>n</i> = 38)	(<i>n</i> = 36)
and Ecuador						
(<i>n</i> _{ai} = 34)						
<i>B. t. auricularis</i> East	20.32 ± 8.38	3.23 ± 1.85	6.55 ± 1.07	3.62 ± 0.53	10.06 ± 0.97	6.42 ± 1.21
Andes, Colombia	(10–54)	(1.34–11.46)	(4.71–9.42)	(2.71–4.83)	(7.62–12.07)	(4.21–8.61)
(<i>n</i> _{ai} = 22)	(<i>n</i> = 37)	(<i>n</i> = 38)	(<i>n</i> = 37)	(<i>n</i> = 37)	(<i>n</i> = 38)	(<i>n</i> = 37)
<i>B. t. 'baezae'</i> eastern	17.61 ± 5.99	3.38 ± 1.26	5.32 ± 0.88	2.72 ± 0.86	10.31 ± 0.49	7.66 ± 0.94
Ecuador and north Peru	(8–29)	(1.77–6.35)	(3.72–7.11)	(1.53–4.29)	(9.73–11.42)	(5.70–9.33)
(<i>n</i> _{ai} = 9)	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 15)	(<i>n</i> = 15)
<i>B. t. tristriatus</i> Peru south	22.15 ± 7.79	3.78 ± 1.79	6.30 ± 1.93	3.15 ± 0.70	11.01 ± 0.55	7.86 ± 0.83
of Marañón to Apurímac	(11–36)	(2.16–7.99)	(4.43–10.99)	(2.16–4.11)	(9.79–11.76)	(6.59–9.31)
(<i>n</i> _{ai} = 5)	(<i>n</i> = 13)	(<i>n</i> = 13)	(<i>n</i> = 13)	(<i>n</i> = 13)	(<i>n</i> = 13)	(<i>n</i> = 13)
<i>B. t. subsp.</i> Peru,	15.63 ± 9.02	2.90 ± 1.61	5.35 ± 0.86	3.36 ± 0.60	10.87 ± 0.65	7.51 ± 0.93
Apurímac south	(8–34)	(1.42–6.37)	(4.28–7.09)	(2.39–4.20)	(9.85–11.63)	(6.12–9.24)
(<i>n</i> _{ai} = 4)	(<i>n</i> = 8)	(<i>n</i> = 8)	(<i>n</i> = 8)	(<i>n</i> = 8)	(<i>n</i> = 8)	(<i>n</i> = 8)
<i>B. punctipectus</i> group	12.75 ± 6.66	2.73 ± 1.31	4.63 ± 0.92	4.01 ± 1.04	9.11 ± 1.27	5.10 ± 2.11
Bolivia	(3–31)	(0.54–6.52)	(2.67–6.08)	(1.66–5.68)	(6.95–5.68)	(2.31–9.70)
(<i>n</i> _{ai} = 21)	(<i>n</i> = 36)	(<i>n</i> = 36)	(<i>n</i> = 36)	(<i>n</i> = 36)	(<i>n</i> = 36)	(<i>n</i> = 36)
<i>B. trifasciatus nitidior</i>	7.29 ± 3.31	1.11 ± 0.49	6.59 ± 1.67	2.52 ± 0.68	7.85 ± 0.63	5.43 ± 0.89
Ecuador	(3–14)	(0.55–2.29)	(4.77–11.82)	(1.63–4.66)	(6.32–9.18)	(3.06–6.63)
(<i>n</i> _{ai} = 8)	(<i>n</i> = 17)	(<i>n</i> = 17)	(<i>n</i> = 17)	(<i>n</i> = 16)	(<i>n</i> = 17)	(<i>n</i> = 16)
<i>B. t. trifasciatus</i> Peru	7.68 ± 7.68	1.04 ± 0.97	6.61 ± 1.73	1.92 ± 0.56	7.83 ± 0.78	5.90 ± 0.86
(<i>n</i> _{ai} = 6)	(2–28)	(0.29–3.70)	(3.91–10.29)	(1.04–2.99)	(6.78–9.87)	(4.68–8.10)
	(<i>n</i> = 15)	(<i>n</i> = 15)	(<i>n</i> = 15)	(<i>n</i> = 15)	(<i>n</i> = 15)	(<i>n</i> = 15)

Rising songs

Taxon	NNT	NNS	SLT (s)	SLS (s)	SL (s)	SST (notes/s)
<i>B. t. bessereri</i>	10.72 ± 4.61	19.89 ± 5.43	1.33 ± 0.51	2.21 ± 0.60	3.54 ± 0.72	7.96 ± 0.80
Coastal Cordillera,	(6–20)	(10–30)	(0.77–2.34)	(1.14–3.49)	(2.73–5.32)	(6.26–9.95)
Venezuela	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 18)	(<i>n</i> = 18)
(<i>n</i> _{ai} = 6)						

<i>B. t. meridanus</i> Mérida, Venezuela (n_{ai} = 4)	12.40 ± 4.38 (6–17) ($n = 10$)	13.70 ± 5.96 (6–23) ($n = 10$)	1.44 ± 0.54 (0.80–2.22) ($n = 10$)	1.39 ± 0.62 (0.57–2.46) ($n = 10$)	2.83 ± 0.31 (2.39–3.34) ($n = 10$)	8.71 ± 1.58 (7.27–12.45) ($n = 10$)
<i>B. t.</i> subsp. San Lucas ($n_m = 1$)	8 ($n = 1$)	18 ($n = 1$)	0.76 ($n = 1$)	2.28 ($n = 1$)	3.04 ($n = 1$)	10.51 ($n = 1$)
<i>B. t. daedalus</i> Central Andes ($n_m = 16$)	17.91 ± 4.66 (11–28) ($n = 23$)	19.96 ± 3.07 (16–25) ($n = 27$)	1.39 ± 0.28 (0.92–1.74) ($n = 28$)	2.06 ± 0.56 (1.09–3.14) ($n = 27$)	3.45 ± 0.68 (2.66–4.81) ($n = 27$)	13.13 ± 1.93 (10.18–16.93) ($n = 24$)
<i>B. t. daedalus</i> West Andes, Colombia, and west slope, Colombia and Ecuador ($n_m = 18$)	18.03 ± 3.74 (12–26) ($n = 37$)	27.74 ± 6.19 (14–42) ($n = 38$)	1.20 ± 0.26 (0.71–1.70) ($n = 37$)	2.22 ± 0.57 (1.22–3.42) ($n = 38$)	3.34 ± 0.64 (2.04–4.63) ($n = 38$)	16.36 ± 2.31 (11.08–19.69) ($n = 37$)
<i>B. t. auricularis</i> East Andes, Colombia ($n_m = 26$)	37.18 ± 8.03 (16–53) ($n = 38$)	20.78 ± 5.36 (6–33) ($n = 45$)	1.63 ± 0.42 (0.99–2.60) ($n = 49$)	1.56 ± 0.43 (0.39–3.32) ($n = 48$)	3.19 ± 0.42 (2.35–4.39) ($n = 48$)	21.24 ± 2.92 (14.13–27.96) ($n = 18$)
<i>B. t. 'baezae'</i> eastern Ecuador and north Peru ($n_m = 13$)	37.20 ± 6.46 (24–47) ($n = 25$)	18.12 ± 5.89 (0–29) ($n = 26$)	1.81 ± 0.30 (1.23–2.31) ($n = 27$)	1.52 ± 0.41 (0.00–2.72) ($n = 26$)	3.31 ± 0.48 (2.11–4.32) ($n = 27$)	20.76 ± 1.28 (18.77–23.81) ($n = 26$)
<i>B. t. tristriatus</i> Peru south of Marañón to Apuímac ($n_m = 7$)	28.0 ± 8.52 (18–44) ($n = 17$)	24.94 ± 7.28 (11–39) ($n = 16$)	1.38 ± 0.35 (0.89–2.10) ($n = 19$)	1.72 ± 0.64 (1.00–3.26) ($n = 20$)	3.11 ± 0.66 (2.39–4.54) ($n = 19$)	19.20 ± 2.15 (15.81–23.78) ($n = 17$)
<i>B. t.</i> subsp. Peru Apuímac south ($n_m = 4$)	23.1 ± 6.92 (15–33) ($n = 10$)	24.13 ± 5.17 (18–30) ($n = 8$)	1.36 ± 0.38 (0.85–1.91) ($n = 10$)	2.61 ± 0.40 (2.07–3.20) ($n = 8$)	4.03 ± 0.21 (3.69–4.35) ($n = 8$)	16.93 ± 0.78 (15.72–18.32) ($n = 10$)
<i>B. punctipectus</i> group Bolivia ($n_m = 36$)	19.29 ± 3.46 (12–25) ($n = 34$)	6.81 ± 4.39 (0–19) ($n = 37$)	2.35 ± 0.47 (1.37–3.13) ($n = 52$)	0.91 ± 0.70 (0.00–3.78) ($n = 46$)	3.23 ± 0.92 (1.87–6.67) ($n = 46$)	7.72 ± 1.10 (5.42–9.52) ($n = 34$)
<i>B. trifasciatus nitidior</i> Ecuador ($n_m = 13$)	/	26.47 ± 5.08 (11–34) ($n = 32$)	/	/	2.57 ± 0.59 (1.14–4.39) ($n = 33$)	/
<i>B. t. trifasciatus</i> Peru ($n_m = 8$)	/	23.77 ± 5.61 (14–35) ($n = 13$)	/	/	2.71 ± 0.50 (1.76–3.53) ($n = 14$)	/
Taxon	SSS (s)	mFT (kHz)	MFT (kHz)	FVT (kHz)	mFT (kHz)	MFT (kHz)
<i>B. t. bessereri</i> Coastal Cordillera, Venezuela ($n_m = 6$)	9.03 ± 1.15 (7.58–11.96) ($n = 18$)	5.50 ± 0.46 (4.43–6.33) ($n = 18$)	7.48 ± 0.63 (6.04–8.64) ($n = 18$)	1.98 ± 0.82 (0.71–4.21) ($n = 18$)	3.70 ± 0.63 (2.37–4.18) ($n = 18$)	10.32 ± 0.96 (8.61–12.25) ($n = 18$)
<i>B. t. meridanus</i> Mérida, Venezuela (n_m = 4)	9.94 ± 0.62 (9.35–11.14) ($n = 10$)	5.52 ± 0.15 (5.33–5.84) ($n = 10$)	7.44 ± 0.47 (6.59–8.28) ($n = 10$)	1.92 ± 0.44 (1.13–2.63) ($n = 10$)	4.42 ± 0.69 (3.62–5.59) ($n = 10$)	9.37 ± 0.65 (8.18–10.22) ($n = 10$)
<i>B. t.</i> subsp. San Lucas ($n_m = 1$)	7.63 ± 0.37 (7.37–7.89) ($n = 2$)	5.93 ($n = 1$)	6.51 ($n = 1$)	0.58 ($n = 1$)	5.10 ± 0.08 (5.05–5.16) ($n = 2$)	9.58 ± 0.10 (9.51–9.66) ($n = 2$)
<i>B. t. daedalus</i> Central Andes ($n_m = 16$)	10.14 ± 2.22 (7.30–15.60) ($n = 27$)	5.21 ± 0.34 (4.73–6.01) ($n = 29$)	6.78 ± 0.44 (6.01–7.75) ($n = 29$)	1.57 ± 0.22 (1.17–1.92) ($n = 28$)	3.87 ± 0.23 (3.30–4.16) ($n = 28$)	9.87 ± 0.63 (8.98–11.08) ($n = 28$)
<i>B. t. daedalus</i> West Andes, Colombia, and west slope, Colombia and Ecuador ($n_m = 18$)	12.73 ± 2.0 (8.71–17.96) ($n = 38$)	5.34 ± 0.35 (4.68–5.98) ($n = 38$)	6.74 ± 0.49 (5.65–7.74) ($n = 37$)	1.40 ± 0.35 (0.85–2.16) ($n = 36$)	3.30 ± 0.67 (1.80–4.46) ($n = 39$)	6.70 ± 1.35 (3.29–9.34) ($n = 39$)
<i>B. t. auricularis</i> East Andes, Colombia ($n_m = 22$)	13.58 ± 2.42 (9.93–20.07) ($n = 45$)	4.96 ± 0.41 (3.05–5.61) ($n = 49$)	6.72 ± 0.42 (5.92–7.66) ($n = 50$)	1.74 ± 0.55 (0.92–3.34) ($n = 48$)	4.09 ± 0.57 (2.72–4.94) ($n = 47$)	9.69 ± 0.76 (7.34–11.15) ($n = 45$)

<i>B. t. 'baezae'</i> eastern Ecuador and north Peru (<i>n</i> _{ai} = 9)	12.15 ± 2.36 (8.77–18.17) (<i>n</i> = 26)	5.03 ± 0.20 (4.79–5.61) (<i>n</i> = 28)	6.89 ± 0.31 (6.07–7.37) (<i>n</i> = 28)	1.86 ± 0.31 (1.28–2.37) (<i>n</i> = 28)	3.46 ± 0.61 (1.82–4.67) (<i>n</i> = 26)	9.75 ± 0.64 (8.54–10.98) (<i>n</i> = 26)
<i>B. t. tristriatus</i> Peru south of Marañón to Apurímac (<i>n</i> _{ai} = 7)	14.81 ± 3.53 (10.66–20.87) (<i>n</i> = 16)	5.16 ± 0.16 (4.77–5.41) (<i>n</i> = 19)	6.64 ± 0.36 (6.09–7.24) (<i>n</i> = 20)	1.46 ± 0.28 (1.03–2.13) (<i>n</i> = 19)	3.60 ± 0.46 (2.60–4.20) (<i>n</i> = 19)	10.34 ± 0.62 (9.06–11.12) (<i>n</i> = 20)
<i>B. t.</i> subsp. Peru Apurímac south (<i>n</i> _{ai} = 4)	9.23 ± 1.24 (7.55–11.10) (<i>n</i> = 8)	5.23 ± 0.16 (5.01–5.53) (<i>n</i> = 11)	6.94 ± 0.43 (6.49–7.55) (<i>n</i> = 11)	1.71 ± 0.38 (1.28–2.28) (<i>n</i> = 11)	3.62 ± 0.66 (2.93–4.38) (<i>n</i> = 9)	9.97 ± 0.48 (9.38–10.98) (<i>n</i> = 9)
<i>B. punctipectus</i> group Bolivia (<i>n</i> _{ai} = 21)	7.47 ± 2.45 (4.68–14.04) (<i>n</i> = 36)	3.51 ± 0.20 (3.14–4.08) (<i>n</i> = 63)	6.40 ± 0.58 (5.19–7.74) (<i>n</i> = 62)	2.89 ± 0.62 (1.70–4.29) (<i>n</i> = 62)	3.27 ± 1.09 (1.60–5.25) (<i>n</i> = 34)	9.59 ± 1.41 (6.97–12.05) (<i>n</i> = 34)
<i>B. trifasciatus nitidior</i> Ecuador (<i>n</i> _{ai} = 13)	10.61 ± 1.21 (8.60–13.73) (<i>n</i> = 32)	/	/	/	3.63 ± 0.70 (2.19–4.82) (<i>n</i> = 33)	9.56 ± 0.82 (8.05–12.43) (<i>n</i> = 33)
<i>B. t. trifasciatus</i> Peru (<i>n</i> _{ai} = 8)	8.71 ± 0.97 (7.60–10.31) (<i>n</i> = 13)	/	/	/	3.94 ± 0.60 (3.08–5.21) (<i>n</i> = 14)	9.98 ± 1.17 (7.95–11.86) (<i>n</i> = 14)

Appendix 3: Materials examined

All specimens, sound-recordings and other records used in analyses are cited. For sound-recordings, coordinates are taken from relevant database, publication or recordist.

Specimens.—All were personally examined, as were all *B. basilicus*, *B. trifasciatus* and non-Colombian *B. tristriatus* at AMNH, BMNH and USNM. Some specimen data are based on Biomap Alliance Participants (2012). Other Colombian specimens of *B. tristriatus* are detailed in Biomap Alliance Participants (2012).

***B. basilicus* Santa Marta, Colombia** ICN 23442–447 (San Pedro, Quebrada Cebolleta, Santa Marta, Magdalena). 23448 (San Lorenzo, Santa Marta, Magdalena).

B. melanotis:

***B. m. melanotis* Costa Rica and western Panama** AMNH 131013 (Chiriquí, Panama), 154391, 391969–670, 505641–643 (paratypes, Aquinares, Costa Rica), 505639 (Chiriquí, Panama), 505640 (Costa Rica). BMNH 1885.3.8.667 (Costa Rica), 1898.12.1.826. 1899.12.1.100–103 (all, Azahar de Cartago, Costa Rica), 1900.7.30.46 (La Hondura), 1919.58.807 (Cachí, Costa Rica),

***B. m. chitreusis* Panama** AMNH 187748–749, 246437, 246439–453 (paratypes, Chitrá). BMNH 1885.3.8.668–669 (Cordillera Chucú, Veraguas).

***B. tacarcunae* Panama** AMNH 136199–201, 136204–212 (paratypes, Mt. Tacarcuna, Panama). **Colombia** ICN 37370 (Acandé, Cerro Tacarcuna, Chocó), 38182 (Unguía, Chocó).

B. tristriatus:

***B. t. pariae* Paria Peninsula, Venezuela** AMNH 44323, 44315 (Cerro Humo), 40587 (Cerro Azul).

***B. t.* subsp. Serranía de San Lucas, Colombia** ICN 34167, 34178 (La Punta, Santa Rosa del Sur, Bolívar).

***B. t. auricularis* East Andes and head of Magdalena Valley, Colombia** AMNH 17448–450 (La Candela, Huila), 50630–631 and three others ('Bogotá'), 122666 (Aguadita, Cundinamarca). BMNH 1884.5.15.420 ('Bogotá'), 1885.3.8.666 (co-type, 'vicinity of Bogotá, New Grenada'), 1921.12.29.112 (San Agustín, Huila), 1921.12.29.113, 1921.12.29.168 (La Candela, Huila). ICN 3720, 4221–222 (Aguadita, Fusagasugá, Cundinamarca), 17409–413, 25552, 25620, 25622, 25630 (Corinto, Comioque, Pajarito or río Cusiana, Boyacá), 25098 (Cañaverales / Virolín, Charalá, Santander), 25390, 25393–394 (Loma del Rayo, Virolín / Charalá, Santander), 27008 (La Cascada, Acevedo, PNN Cueva de los Guacharos, Huila), 30929 (3 km north-east of Monteredondo, Guayabetal, Cundinamarca), 32620 (Aguas Claras, Cubarral, Meta), 32987 (La Grilla, Serranía de las Quinchas, Otanche, Boyacá), 33155 (El Retiro, Campo Hermoso, Ubatá, Boyacá), 33443 (Serranía de los Churumbelos, Cauca), 34365 (El Talismán, San Vicente de Chucurí, Serranía de los Yariguíes, Santander), 34985 (El Mortiño, Floridablanca, Santander), 35218 (Finca La Argentina, Virolín, Charalá, Santander), 35321, 35324, 36447 (La Pajarita, Tona, Bucaramanga), 36323 (Suratá, Bucaramanga), 37067 (El Cinco, Manaure, Serranía de Perijá, Cesar), 37159–160, 37197–198 (San Antonio, Manaure, Serranía de Perijá, Cesar), 37310 (La Aurora, Galán, Serranía de los Yariguíes, Santander), 37325 (Piedecuesta, Santander). UIS unnumbered (2) (Tona, Santander), unnumbered (believed to be near Charalá, Santander). USNM 88398 ('Bogotá'), 369875 (Monte Elias, Fonseca, Guajira), 374780–802 (Laguna de Junco, Jagua del Pilar, Guajira), 374779 (Virolín, Charalá,

Santander), 374783–788 (La Africa, Villanueva, Guajira), 398976–987 (Buenos Aires, Bucarasica, Norte de Santander), 412262, 412564 (Hacienda Las Vegas, Piedecuesta, Santander), 403423–425 (Villa Felisa, Cúcuta, Norte de Santander), 447435–436 (Belén, La Plata, Huila).

B. t. daedalus **Central Andes, Colombia** AMNH 109164–168, 109327–330 (east of Palmira, Valle del Cauca), 113257–259 (Salento, Quindío), 113260–262 (El Roble, Circasia, Quindío), 113258 (Páramo de Santa Isabel, Risaralda / Tolima / Caldas), 134101 (La Frijolera, Antioquia). BMNH 1921.12.29.114 (Salento, Quindío). ICN 34376 (Retiro, Antioquia), 34587 (El Encanto, La Secreta, Amalfi, Antioquia), 34531 (Salazar, Finca Bodega Vieja, Amalfi, Antioquia), 34546 (Santa Gertrudis Vereda, Anorí, Antioquia), 34597, 34602, 34624 (Bosque La Escuela, Amalfi, Antioquia), 37295–296, 37298, 37301 (Filandia, Vereda La Julia, Quebrada los Picos, Quindío). USNM 403426–433 (Valdivia, Antioquia), 436884–887 (La Bodega, Antioquia), 436888–891 (Hacienda La Sofia, río Samaná, Caldas).

B. t. daedalus **West Andes and west slope, Colombia** AMNH 108386–390, 108647, 109162–163, 109332, 511391 (San Antonio, La Cumbre, Valle del Cauca), 108391–392 (Lomitas, La Cumbre, Valle del Cauca), 109976 (Cocal, El Tambo, Cauca), 109977, 110288–290 (Cerro Munchique, El Tambo, Cauca), 110291–293, 109973–735 (Gallera, west of Popayán, Cauca). ICN 17522–223, 32286 (Almaguer, Barbacoas, Nariño), 27284 (Reserva Natural La Planada, Ricaurte, Nariño), 25840, 25873, 25875–876, 25881, 25891 (Corea, PNN Farallones de Cali, Valle del Cauca), 35684 (La Messania, Finca Primavera, Jardín, Antioquia), 37461 (20 de Julio, El Tambo, Cauca), 37487 (Reserva Natural Río Nambí, Nariño). USNM 427317–320, 427324 (Hacienda Potreros, Frontino, Antioquia). **Ecuador** BMNH 1884.5.15.418, 1884.5.15.419, 1885.3.8.672 (Pallatanya) 1901.4.25.44–45 (Posvenio, Bolívar), 1916.8.24.79 (Mindó, Pichincha), 1925.12.24.451 (Tandapi), 1938.12.20.94 (río Saloya), 1953.68.595 (Guayupe, Imbabura, 1,250 m), 1953.68.808 (Chaspé).

B. t. 'baezae' **Ecuador** AMNH series examined but not measured. BMNH 1884.12.9.1–2 ('Trisbrunfoncé ellachay'), 1885.2.8.7 (Machay), 1901.4.25.46 (Mirandar, Baños), 1925.12.24.450 (Baeza), 1953.68.809 (Abanico Oriente, 1,600 m).

B. t. tristriatus **Peru** AMNH 820244 (Cordillera Vilcabamba, Cusco), 82087–096 (Cerros de Sira, Huánuco). BMNH 1903.10.17.12 (Cusco).

B. punctipectus group **Bolivia** AMNH 823900 (15 km north of Monte Punco, Totora, Cochabamba), 823901–902 (río Vanimayo, Yungas de Totora, 30 km north of Monte Punco, Cochabamba). BMNH 1885.3.8.664, 1885.3.8.666 (Simacu).

Sound recordings.—Acronyms as follows: XC = www.xeno-canto.org; IAVH = Instituto Alexander von Humboldt's Colección de Sonidos Ambientales; ML = Macaulay Library, Cornell Lab of Orn.; AV = AVoCet www.avocet.zoology.msu.edu. Localities are listed north to south by taxon and then by country.

B. basilicus **Songs.**—RNA El Dorado or San Lorenzo ridge, Santa Marta, Magdalena (11°06'N, 74°03'W) (Krabbe 2008, disc 2: 62(1–4); XC43566: T. M. Donegan; XC165599, 165611: A. Spencer; XC117717–718: M. Álvarez; XC102579: F. Schmitt). **Calls.**—Krabbe (2008, disc 2: 62(3–5) (as 62(1–4))).

B. m. melanotis **Costa Rica** **Songs.**—90 km north-west of San José, Monteverde, Puntarenas (10°18'N, 84°05'W; 1,600 m) (ML32713: L. F. Kibler). Bosque de Paz Biological Reserve (10°12'N, 84°21'W) (XC107255–257: M. Nelson). Monteverde Cloudforest Preserve, Guanacaste (ML32284: T. A. Parker; ML76716: C. A. Marantz; Ross & Whitney 1995, disc 2: 74). **Calls.**—AV13925 (as ML32284 but P. C. Rasmussen). ML39207 (as ML32284). ML76707 (as ML76717). ML72827 (as ML76716 but D. Ross). ML32713 (as above). XC107255–257 (as above).

B. m. chitrensis **Panama** **Songs.**—Cerro Colorado, Comarca Ngobe-Bugle (formerly Chiriquí) (08°32'N, 81°48'W; 1,600 m) (XC145616–617: W. Adsett).

B. tacarcunae **Panama** **Song.**—Sitio de Guillen, Chagres National Park (09°19'N, 79°18'W, 750 m) (XC145623: W. Adsett).

B. tristriatus

B. t. bessaeri **Venezuela, Coastal Cordillera** **Rising songs.**—Oripoto, Miranda (10°26'N, 66°50'W; 1,200 m) (ML67198–99: P. A. Schwartz). Colonia Tovar, Aragua (10°24'N, 67°20'W; 1,800–2,200 m) (ML53618: L. R. Macaulay; Boesman 1999: 25.2 = Boesman 2012: 3197–3). Rancho Grande, km 20.5, Aragua (10°22'N, 67°41'W; 1,100 m) (ML67202: P. A. Schwartz). Sierra de Aroa, Yaracuy, Venezuela (10°20'N, 68°50'W) (Boesman 2012 track 3197–6). **Slow songs.**—Boesman 1999: 25.2, ML67202 (see above). **Calls.**—Parque Nacional El Ávila, Camino de los Españoles, Distrito Federal (10°33'N, 66°56'W) (ML127798: C. A. Marantz). ML67200 (as ML67198). Boesman (1999: 25.2) (as above). Boesman (2012: 3197–6) (as above).

B. t. meridaui **Venezuela** **Songs.**—Parque Nacional Yacambú, Lara (09°43'N, 69°35'W; 1,300–1,750 m) (Boesman 1999: 25–1 = Boesman 2012: 3197–1). San Isidro quarry, Barinas (08°50'N, 70°35'W; 1,500 m) (XC65916: D. F. Lane). South of Santo Domingo Valley, Barinas (08°32'N, 70°30'W; 1,355 m) (ML102505: L.

R. Macaulay). 13 km east of Santo Domingo, Barinas (08°32'N, 70°30'W; 550 m) (ML52699: S. L. Hilty). *Slow songs*.—Boesman (1999: 25-1), XC65916, ML52699, 102505 (as above). *Calls*.—ML52699 (as above). Boesman (1999: 25.3) = Boesman (2012: 3197-7) (as 25.1).

B. t. subsp. Serranía de San Lucas, Colombia *Rising song*.—Santa Cecilia, Santa Rosa del Sur, Bolívar (07°58'33"N, 74°12'55"W; 1,550 m) (XC176120: T. M. Donegan). *Slow songs*.—XC176120 (as above), XC92160, 176116 (both as XC176120). *Calls*.—XC92160, 104230, 176116, 176118, 176119 (all as XC176120).

B. t. daedalus Central Andes, Colombia *Rising songs*.—Vereda Corcovado, Finca Villa Nueva, Antioquia (07°03'N, 75°27'W; 2,100 m) (XC131770: O. H. Marín-Gómez). Reserva La Forzosa, Anorí, Antioquia (07°00'N, 75°09'W; 1,550 m) (XC55260: B. López-Lanús). La Romera, Medellín, Antioquia (Boesman 2012: 1696-1, 3197-4-5). Hacienda Termópilas, Neira, Caldas (05°14'N, 75°29'W; 2,250 m) (IAVH7905: S. Córdoba; IAVH7979: M. Álvarez). Campo Alegrito, Santa Rosa de Cabal, Risaralda (04°52'N, 75°33'W; 2,380 m) (IAVH 15356-357: S. Córdoba). SFF Otún Quimbaya, Risaralda (04°44'N, 75°35'W; 1,875 m) (XC105650, 105659: E. de Fonso). AICA La Patasola, Salento, Quindío (04°41'N, 75°33'W, 2,300 m) (XC128598: O. H. Marín-Gómez). Reserva Bremen, Buenavista, Quindío (04°20'N, 75°44'W) (IAVH 7293: M. Álvarez; XC128994-997, 128999 (all treated as same recording), 130016, 130020, 130032 (all treated as same recording), 131163 (apparent subsong): O. H. Marín-Gómez). *Slow songs*.—Amalfi, vereda Guayabito, Antioquia (06°59'N, 75°04'W) (Álvarez *et al.* 2007, disc 7: 51d). Boesman (2012: 1696-1, 3197-4-5, as above). IAVH 7905, 15356-357 (as above). XC55262 (as XC55260), XC105654 (as XC105650). XC128531 (as XC128994). XC105650, 128994-995, 130016, 130020, 130032 (latter three same recording but multiple individuals), 131770 (as above). *Calls*.—La Suiza, SFF Otún-Quimbaya, Risaralda (1,700 m) (XC53954: B. López-Lanús). XC128553 (as XC128994). Álvarez *et al.* (2007, disc 7: 51d) (as above). IAVH 7979, 15357 (both, as above). XC102559 (as XC105659, J. Minns). XC130440, XC130714 (both as XC128994), XC105654, 105659, 128531, 128598, 130016, 130020, 130032 (all as above). Boesman (2012: 1696-1, 3197-5, as above). *Juvenile calls*.—XC131767-768 (as XC131770).

B. t. daedalus West Andes / west slope *Rising songs*.—**Colombia** Reserva Natural Mesenia (05°29'N, 75°54'W; 2,000 m) (XC96010: O. Cortes). Apía, Risaralda (05°10'N, 76°19'W; 2,200-2,360 m) (IAVH 15899: S. Córdoba). Near RNA Las Tangaras, Chocó (05°43'N, 76°15'W; 1,800 m) (ML165277: M. J. Sarver). El 18, Valle del Cauca (03°29'N, 76°37'W) (XC22420 = Boesman 2012: 3197-2: A. Spencer). Altaquer, Reserva Natural Río Nambí, Nariño (01°18'N, 78°05'W; 1,100-1,600 m) (XC12378, 12755-556, 13152; latter three treated as same recording: O. Laverde). Ricaurte, Reserva Natural La Planada, Nariño (01°05'N, 77°53'W; 2,000 m) (XC12747: O. Laverde; Álvarez *et al.* 2007, disc 7: 51a). **Ecuador** Maldonado Road, Carchi (00°57'N, 78°12'W; 1,550 m) (Krabbe & Nilsson 2003: 31-1). Hacienda la Florida, Imbabura (00°22'N, 78°29'W; 2,000 m) (Krabbe & Nilsson 2003: 31-2). Barcelona, Cordillera Toisan, Imbabura 00°20'N, 78°36'W; 1,850 m) (Krabbe & Nilsson 2003: 31-4). Reserva Maquipacuna, Pichincha (00°05'N, 78°37'W; 1,600 m) (ML58048-049, treated as same recording: P. Coopmans). Tandayapa Lodge, Pichincha (00°00'N-00°06'N, 78°40'W; 1,820-1,850 m) (XC6717, 16092: N. Athanas; Krabbe & Nilsson 2003: 31-3). Reserva Las Tangaras, Mindo, Pichincha (00°05'S, 78°47'W; 1,400 m) (XC164158, 165091: M. St. Michel). Tandayapa Valley, Pichincha (00°01'S, 78°41'W; 1,200 m) (XC112289: T. Brooks). Mindo, Pichincha (00°00'S, 78°47'W; 1,200 m) (XC118021, 118023-024: E. de Fonso). Calacali-Nanegalito road, Pichincha (Moore *et al.* 1999, disc 3: 17-1). *Slow songs*.—**Colombia** Anchicayá Valley, Valle del Cauca (03°32'N, 76°48'W; 1,000 m) (ML83777: S. L. Hilty). Alto de Pisones, Risaralda (05°18'N, 75°56'W) (IAVH11193 / XC148264: F. G. Stiles). ML165277 (as above). XC96010 (as above). **Ecuador** Mashpi Road, Pichincha (00°10'N, 78°51'W; 1,200 m) (XC58007: C. Vogt). Old Chiriboga Road, Pichincha (00°15'S, 78°45'W; 1,800 m) (XC4000: D. Jones; Moore *et al.* 1999, disc 3: 17-3). Krabbe & Nilsson (2003: 31-2) (as above). ML58048 (as above). XC5061, 6639, 32031 (all as XC6717), XC112289, 118023-024, 164518, 165091 (all, as above). XC163525, 168841 (both as XC164518). *Calls*.—**Colombia** PNN Tatamá, Pueblo Rico, Risaralda (05°14'N, 76°05'N; 1,600 m) (Boesman 2012: 3197-8). Reserva Natural Cerro el Inglés, Valle del Cauca (04°44'N, 76°18'W; 1,900 m) (XC22422: A. Spencer). El Cairo, Serranía de los Paraguas, Valle del Cauca (04°18'N, 76°13'W) (Álvarez *et al.* 2007, disc 7: 51a-b) (as above). Territorio Kofán, Ipiales, Nariño (00°28'N, 77°17'W, 800-1,450 m) (XC117226 = IAVH137: M. Álvarez). ML83777, 165277 (both as above). XC12377, 13153 (both as XC12755). XC24421 (as XC24420). XC96010 (as above). XC95883 (as XC96010). IAVH11193 / XC148264 (as above). IAVH11192 (= XC148263), IAVH11202 (=XC148272) (both as IAVH11193 / XC148264). **Ecuador** Cabañas San Isidro, Napo (00°35'S, 77°53'W; 2,130 m) (XC95024: D. F. Lane). Krabbe & Nilsson (2003: 31-2) (as above). Moore *et al.* (1999, disc 3: 17-1-2) (both, as 17-1). ML80985 (as ML58048 but D. Ross). ML58048-049 (as above). XC6632, 9860 (as XC 6717). XC118039 (as XC118023). XC4000, 112289, 163525, 168841 (all as above). *Juvenile begging call*.—XC58002 (as XC58007).

B. t. auricularis East Andes and head of Magdalena Valley, Colombia *Rising songs*.—Sisavita, Carrizal, Cucutilla, Norte de Santander (07°29'N, 72°50'W; 2,150 m) (XC117539 (= IAVH9044), IAVH9098: S. Córdoba). RNA Reinita Cielo Azul, San Vicente de Chucurí, Santander (as 'El Talismán' below, but 1,900 m) (Boesman 2012: 151-2, 625-4, 1252-4). La Luchata, above Galán, Serranía de los Yariguíes, Santander (06°38'N, 73°19'W; 2000 m) (XC30819, 30821, 30823, treated as same recording, 30850-852, treated as same recording, 31694: T. M. Donegan). La Aurora, above Galán, Serranía de los Yariguíes, Santander (06°38'N, 73°23'W; 2,700 m) (XC25497, 25501-502, 25508-509, 25511-514, 25518, 25530, 25533-335 [from 25501 on treated as same recording]: T. M. Donegan). Medina, Cundinamarca (04°35'N, 73°26'W; 1,480-1,800 m) (ML80870, 80874,

80876, latter two treated as same recording, 80923–924 = Álvarez *et al.* 2007, disc 7: 51c; XC117282 = IAVH287: M. Álvarez). PNN Los Picachos, Finca Andalucía, Caquetá (02°48'N, 74°51'W; 1,400 m) (ML89242, 89258 = IAVH455–456: M. Álvarez). PNN Cueva de los Guacharos, Acevedo, Huila (01°37'N, 76°06'W; 1,810–2,100 m) (IAVH6949, 6990, 6991, all treated as same recording, 7006, 7048–49, treated as same recording, 7057, 7162, 7163, 7166, latter four treated as same recording: M. Álvarez; XC117930 [= IAVH16113]: J. E. Parra). *Slow songs*.—El Talismán, San Vicente, Yariguíes, Santander (06°51'N, 73°22'W; 2,000 m) (XC24162: T. M. Donegan). Boesman (2012: 151–2, as above). IAVH8641 (as IAVH9098), IAVH6990, 7057, 9098 (all as above). ML80870, 80923–924, 89242, 89258 (all as above). ML80940 (as ML80870). XC25476, 25501–503 (treated as same recording), 25508, 25512, 25514 (all as XC25497). XC30821, 30850, 31694, 117539 (all as above). *Calls*.—SFF Iguaque, Chiquiza, Boyacá (05°38'N, 73°82'W, 3,000 m) (XC117231 = IAVH 1175: M. Álvarez). Río Yurayaco, San José de la Fragua, Caquetá (01°21'N, 76°08'W, 1,000–1,500 m) (IAVH 4306: M. Álvarez). IAVH 6990, 6991, 7006, 7166 (all as above). IAVH 9087 (as IAVH 9098). IAVH9098. ML89385 = IAVH457 (as ML89242). ML80870, 80876, 80923–234, 80940 (all as above). XC34943 (as XC30819). XC24289 (as XC24162). XC25417 (as XC25418), XC117933–334 (as XC117930). XC25501–502, 25880–881, 117539 (as above).

B. t. 'baezae' Ecuador, east slope, and Peru, east slope south to Huancabamba depression *Rising songs*.—**Ecuador** Hacienda San Isidro, 2 km south-west of Cosanga, Napo (00°35'S, 77°53'W; 2,100 m) (Krabbe & Nilsson 2003: 31–5). San Isidro Lodge, Napo (00°40'S, 77°55'W) (Boesman 2012: 1809–2). Cordillera Guacamayos, Napo (00°37'S, 77°49'W; 1,700–2,150 m) (Krabbe & Nilsson 2003: 31–7). Quebrada las Ollas, Santa Barbara–La Bonita road, Sucumbíos (00°33'N, 77°32'W; 2,150 m) (Krabbe & Nilsson 2003: 31–6). Cordillera Cutucú, Morona-Santiago (02°39'S, 78°08'W; 1,550 m) (ML36050: T. S. Schulenberg). Cordillera de Cutucú, Morona-Santiago (02°43'S, 78°05'W; 2,012 m) (ML41278: M. B. Robbins). Cordillera del Condor, Morona-Santiago (03°29'S, 78°14'W; 1,500 m) (ML72789, 78023, 78027–028, 78030, 78035, 78050 [all treated as same recording], 78058, 79600, 79619: T. A. Parker). Chinapintza, Cordillera del Condor, Zamora-Chinchipe (04°02'S, 78°38'W; 1,700 m) (XC93378–379, treated as same recording: R. Ahlman). **Peru** East slope of Cerro Chinguela, Lucuma, Cajamarca (05°07'S, 79°23'W) (ML21713: T. A. Parker). *Slow songs*.—**Ecuador** Krabbe & Nilsson (2003: 31–7, as above). ML36050, 78023, 78028, 78030, 78035, 78058 (all as above). XC93378–379 (as above). *Calls*.—**Ecuador** La Sofia road, Sucumbíos (00°26'N, 77°35'W; 2,440 m) (XC93158–159: C. Vogt). West of Cutucú, Morona-Santiago (02°26'S, 78°03'W; 1,900–1,950 m) Krabbe & Nilsson (2003: 31–8). Boesman (2009: 1809–1–2). ML41253 (as ML41278). ML79627 (as ML72789). ML36050, 41278, 72789, 78023, 78027–8, 78030, 78035, 78050, 78058, 79619, 82620 (all as above). Krabbe & Nilsson (2003: 31–7) (as above).

B. t. tristriatus Peru, south of Huancabamba depression to Apurímac *Rising songs*.—Abra Patricia, San Martín (05°50'S, 77°46'W) (Boesman 2009: 1809–1; Boesman 2012: 2005–4). 15 km north-east of Jirillo, San Martín (06°03'S, 76°44'W; 1,350 m) (ML42070: T. S. Schulenberg). Afluente, San Martín (05°40'S, 77°42'W; 1,400 m) (XC141786: D. F. Lane). Camp Utter Solitude, Alto Mayo, San Martín (05°43'S, 77°45'W; 2,150 m) (XC132704: D. F. Lane). North-east of Tingo María, Loreto (09°00'S, 75°00'W) (ML28805: A. B. van den Berg). Cordillera Divisoria, Huánuco (09°10'S, 75°29'W; 1,219 m) (ML31886: T. A. Parker). Below Calabazas, Junín (11°27'S, 74°47'W; 1,400 m) (ML147187: M. B. Robbins). *Slow songs*.—Abra Patricia–Alto Nieva, San Martín (05°42'S, 77°49'W; 2,040 m) (XC20772: N. Athanas). ML28805, 42070 (both as above). XC141786 (as above). *Calls*.—Below Alto Mayo, San Martín (05°34'S, 77°44'W; 1,700 m) (XC141785: D. F. Lane). 15 km north-east of Villa Rica, Pasco (10°43'S, 75°09'W; 1,250 m) (XC105613: D. F. Lane). ML42070 (as above). ML147174 (as ML147187). XC141786 (as above).

B. t. subsp. Peru, from Apurímac south *Rising songs*.—San Pedro, Manu Road, Cusco (13°03'S, 71°33'W; 1,400 m) (XC63185: J. Tobias & N. Seddon; XC88623: D. F. Lane). San Pedro, south-west of Pilcopata on Cosñipata highway, Cusco (13°09'S, 71°20'W; 1,300 m) (ML85067: A. J. Begazo). Manu, Cusco (13°10'S, 71°30'W) (Boesman 2009: 1809–3). *Slow songs*.—Suiza, Manu Road (2,120 m) (XC10973: C. Hesse). Capiri, Marcapata, Cusco (13°25'S, 70°55'W, 1,900 m) (XC22826: D. Geale). Rocotal, Manu Road, Cusco (13°07'S, 71°34'W; 1,800 m) (XC39704: D. Geale). ML85067 (as above). *Calls*.—Boesman (2012: 1809–2, as above). XC22826 (as above). XC57236 (as XC63185 but D. Geale). XC91046 (as XC88623 but O. Cortes). XC85953–954 (as XC85953). ML85067, 147174 (both as above). XC63185 (as above).

B. punctipectus group Bolivia *Rising songs*.—Pilón Lajas Biosphere Reserve, La Paz (15°06'S, 67°32'W; 750–1,450 m) (XC3104, 3116: A. B. Hennessey). Serranía Bellavista, north of Caranavi, La Paz (15°39'S, 67°30'W) (ML13815, 13852, 17128, 17154, 33726: T. A. Parker). As previous (15°41'S, 67°30'W; 1,250–1,650 m) (XC4094: S. K. Herzog). Yungas, La Paz (16°14'S, 67°48'W; 1,600 m) (XC145038, 150560: D. F. Lane). Tunquini Biological Station, Cotapata NP, La Paz (16°12'S, 67°52'W; 1,500–2,000 m) (XC4744: S. K. Herzog). Urpuma, Sandillani, Cotapata NP, La Paz (16°13'S, 67°53'W; 1,950 m) (XC43916, 44231–232, 44395, 44438: T. M. Donegan). Laguna Carachupa, Cordillera Mosetenes, Cochabamba (16°14'S, 66°25'W; 1,200–1,600 m) (XC4732: S. K. Herzog). Apa, near Chulumani (16°18'S, 67°50'W) (XC454: J. van der Woude). Bosque Apa Apa, La Paz (16°21'S, 67°30'W; 1,800 m) (ML132723: P. A. Hosner). West of Villa Tunari, Cochabamba (16°59'S, 65°24'W; 1,524 m) (ML33704: T. A. Parker). Carrasco National Park, Cochabamba (17°09'S, 65°37'W; 1,755 m) (ML87653: A. B. Hennessey). Chapare (Colomi–Villa Tunari road), Cochabamba (17°09'S, 65°42'W; 1,850 m) (ML50610: P. Coopmans). Old road from Cochabamba to Villa Tunari, Carrasco NP, Cochabamba (17°10'S, 65°35'W; 1,500–2,000 m) (XC3433, 3468, 3475–78, 3480–81, 3484, 3538–40, 3546–47, 3561, 3583: S. K. Herzog; note only sample

of best recordings of this long series analysed). Miguelito Pipeline Road, Cochabamba (17°10'S, 65°46'W; 1,700 m) (XC145025, 149120, 155976: D. F. Lane). Miguelito, Cochabamba (17°10'S, 65°47'W; 1,400–1,600 m) (XC1618–19, treated as same recording), 1623, 1625: S. Mayer). *Slow songs*.—Tokoaque, Madidi NP, La Paz (14°37'S, 68°57'W; 2,400 m) (ML121704, 121718: A. B. Hennessey). XC3431 (as XC3433), XC44216, 44234 (both as XC43916). ML13815, 13852, 17128, 17154, 33704, 33726, 50610, 87653, 132723 (all as above). XC1618, 1623, 4732, 43916, 145025, 145038 (all as above). *Calls*.—ML13815, 13852, 17128, 17154, 33704, 33726 (all as above). XC44213, 44216, 44387 (all as XC43916). XC3431, 149120 (both as above). **Peru** *Calls*.—Maruncunca, Puno (14°10'S, 69°14'W; 2,160 m) (XC85953: D. F. Lane) (identification tentative; as discussed in text, some southern Cusco call or slow song recordings listed above may also belong here).

B. trifasciatus nitidior *Rising songs*.—**Ecuador** Manta Real, Azuay (02°34'S, 79°21'W) (ML82620: T. A. Parker; identified as *tristriatus*, possible intermediate with *B. t. daedalus*; not included in analyses). Piñas (03°43'S, 79°41'W; 1,100 m) (XC55829: M. Sánchez). Loja, El Cisne–Ambocas road (03°49'S, 79°30'W; 1,600 m) (XC81322: L. Ordóñez-Delgado). Loja (03°55'S, 79°40'W; 1,250 m) (ML130400: L. Macaulay). Loja–Catamayo road, Loja (03°57'S, 79°16'W) (ML68185: P. Coopmans). San Pedro de la Bendita, Loja (03°57'S, 79°27'W; 1,850 m) (XC86557: D. F. Lane). Tierra Colorada, Loja (04°02'S, 79°56'W; 1,650 m) (Krabbe & Nilsson 2003: 30.1). Loja (04°02'S, 79°11'W, 2,300 m) (XC136043: L. Ordóñez-Delgado). Between Celica and Guachanamá, Loja (04°05'S, 79°57'W; 2,450 m) (Krabbe & Nilsson 2003: 30.2). Celica, Loja (04°06'S, 79°56'W; 1,700 m) (XC6543: N. Athanas). Celica Mountains, Loja (04°07'S, 79°59'W) (XC67696–697: F. Lambert). Bosque Protector El Tundo, Sozoranga, Loja (04°20'S, 79°49'W; 1,700 m) (XC9269: N. Athanas). Sozoranga, Loja (04°20'S, 79°48'W; 1,600 m) (XC20260: C. Vogt). Parroquia El Airo, Espindola, Loja (04°29'S, 79°23'W, 1,800 m) (XC118557: L. Ordóñez-Delgado). *Slow songs*.—**Ecuador** Krabbe & Nilsson (2003: 30.1, as above). XC55829, 67696, 81322, 118557, 118562, 136043 (all as above). ML130400 (as above). *Calls*.—**Ecuador** Krabbe & Nilsson (2003: 30.1–2, as above). ML68185, 130400 (both, as above). XC118562 (as XC118557). XC6543, 67696, 55829, 81322 (all as above).

B. trifasciatus trifasciatus *Rising songs*.—**Peru** Abra Porculla, Piura (05°50'S, 79°30'W) (Boesman 2009: 1808–1–2). Zona Reservada Laquipampa, Lambayeque (06°18'S, 79°28'W; 1,400 m) (XC5177, 5568, 8633, 8646, 8648: W.-P. Vellinga). Bosque Cachil, Cajamarca (07°24'S, 78°47'W, 2,500 m) (XC75966: C. J. Schmitt). *Slow songs*.—**Peru** Abra Porculla, Piura (05°51'S, 79°31'W, 2,100 m) (XC8551: H. van Oosten). Boesman (2009: 1808–2–3) (as 1808–1). XC75965–967 (as XC75966). *Calls*.—**Peru** Huancabamba (05°20'S, 79°32'W, 2,240–3,050 m) (ML21862: T. A. Parker). Boesman (2009: 1808–1–3) (as 1808–1). XC5186–7 (as XC5177). XC75965–967 (as XC75966). XC8551, 8648 (both as above).